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Adopting behavior and breeding biology of avocets: benefits of large broods for good parents?

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by

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ABSTRACT

ADOPTING BEHAVIOR AND BREEDING BIOLOGY OF AVOCETS: BENEFITS OF LARGE BROODS TO GOOD PARENTS?

– SUMMARY OF PH.D. DISSERTATION –

Szabolcs Lengyel

Alloparental care, in which adults provide care for young that are not genetically related to them, is widespread in birds and mammals. Caring for unrelated young appears to decrease the fitness of adopters and thus the behavior is difficult to explain based on classic evolutionary theory. I studied the evolutionary significance of adoption in avocets (*Recurvirostra avosetta*), a large-sized shorebird breeding on alkaline lakes in Hungary between 1998 and 2000. Thirteen percent of the chicks were adopted chicks and 21% of the avocet families contained adopted young. Most adopted chicks left their own family to gain adoption elsewhere, whereas some chicks were left behind by their parents. More chicks survived in larger broods than in smaller ones. The survival of chicks that left their own family and their siblings remaining in the brood did not differ, whereas chicks that were left behind reached the same survival as their siblings in the natal brood. The quality of the adults was also important, because pairs that later adopted chicks laid their eggs earlier, occupied better territories and fledged more young than did non-adopting pairs. Experimentally enlarged broods fledged more young than did modified or control broods in high predation sites. Incubating experimentally enlarged clutches of eggs required higher energy expenditure by parents. Therefore, I concluded that adoption may be a means to increase the size of the brood for certain, high-quality pairs without incurring the costs of producing and incubating more eggs. Adoption appears to provide fitness benefits to the adopting parents via an increase in brood size. However, adoption is not for every adult; several correlative results and indirect evidence suggest that only high quality adults adopt. In conclusion, this study uncovered an interesting complexity underlying an apparently erroneous behavior in the parental care system of avocets. The findings contribute to an understanding of the evolution of the different forms of parental care and throw light on the possible evolutionary mechanisms that led to the current diversity of reproductive strategies in birds.

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CHAPTER 1. ADOPTION AND BROOD AMALGAMATION IN PRECOCIAL BIRDS: A SYNTHESIS

1.1. INTRODUCTION

Parental care theory has undergone a considerable development in recent decades (Clutton-Brock 1991; Rosenblatt & Snowdon 1996). Despite the progress, some aspects of parental care remain puzzling to behavioral biologists. Alloparental care, defined as a form of parental care in which an offspring is cared for by adults other than its genetic parents (Riedman 1982; Skutch 1987), is one of these areas (Alcock 1993). An understanding of alloparental care can contribute to parental care theory in at least two areas. First, the study of alloparental care can enlight the costs or the benefits of caring for additional young, which, as an analogue to a natural experiment, may be helpful in understanding how parents allocate time and energy into their offspring. Second, it can help in understanding the trade-off that parents face in whether to invest into their current offspring or to save some of their reproductive potential for later breeding attempts.

Alloparental care has been reported to occur in over 220 bird species (Brown 1987). Two main forms of alloparental care are (i) helping in a cooperative breeding system (Emlen et al. 1991), and adoption or brood amalgamation. Adoption is defined here as a behavior in which adults, besides caring for their genetic young, provide parental care to genetically unrelated offspring which become part of their family group. This general definition allows the inclusion of post-hatch brood amalgamation often reported in waterfowl (Eadie et al. 1988; Beauchamp 1997), when chicks from several broods mix under the care of one or more females.

There has been considerable confusion in the literature over the terms used to describe adoption and brood amalgamation. In particular, the situations in which groups of young from several broods are reared by one or more adults or mated pairs of adults have been termed as “brood amalgamation”, “brood mixing”, “creches”, “gang broods” and “pods” (**Table 1.**). Most authors have used these terms interchangeably, whereas others reserved the term “gang broods” for situations in which several adults or mated pairs join together with their broods (e.g. Afton & Paulus 1992; Gosser & Conover 2000).

For the purposes of this review, I use the term “adoption” for cases when one or several young transfer from one brood (donor brood) to another (recipient brood), and when the donor brood does not cease to function as a separate functional unit unless the remaining young perish for whatever reason. Furthermore, I will use the term “brood amalgamation” for cases in which all young from the donor brood become integrated in the recipient brood (i.e., young from two or more broods merge) and the donor brood ceases to function as a separate unit. The young in the merged brood can be cared for by one or more adults or mated pairs of adults. Finally, I will use the term “creche” for groups of young aggregated when their parents are not in attendance. Such groups, frequently found in penguins, flamingos, pelicans, gulls, and cormorants, are not brood amalgamations *sensu stricto* because parents typically find their chicks in the creche and restrict parental care to their own chicks. However, the aggregation of chicks may lead to adults providing care to alien young.

Researchers have long hypothesized that parental care is less costly for birds in which chicks are able to feed on their own (nidifugous chicks) than for species that feed their young (nidiculous chicks). Caring for unrelated young, thus, traditionally has been thought to be less costly or even beneficial to adults in species with nidifugous chicks (Pierotti 1988). Numerous notes in the primary literature and species accounts in handbooks (e.g. Johnsgard 1981, 1983; Cramp & Simmons 1983) report anecdotal information on the occurrence of adoption, and reviews exist for some taxa (mammals and birds: Riedman 1982; gulls and terns: Pierotti & Murphy 1987;

Pierotti 1991; waterfowl: Eadie et al. 1988). These reviews concluded that adoption and brood amalgamation are either altruistic behavior or a non-adaptive side effect, but also suggested fitness benefits of this behavior.

For the purposes of this review, I define precocial birds using Nice's (1962) classification as modified by Starck (1993). A species is considered to be precocial if the neonates show locomotory activity soon after hatching. The ability of young to leave the nest after hatching is of crucial importance in the formation of adoption and brood amalgamation. This definition includes superprecocial birds from the family *Megapodiidae*, precocial birds from various families within the orders *Struthioniformes*, *Tinamiformes*, *Craciformes, Galliformes, Anseriformes, Turniciformes*, *Gruiformes*, *Ciconiiformes,* and semiprecocial birds from the families *Laridae* and *Phoenicopteridae* (taxonomy and order of presentation is based on Monroe & Sibley 1993) These taxa include 1029 species, or 11.82% of all bird species (Table II. in Starck 1993). In addition to these species, the review will be extended to include semialtricial or altricial birds from the families *Phalacrocoracidae* (cormorants), *Spheniscidae* (penguins) and *Pelecanidae* (pelicans) for two reasons. First, chicks of these species are mobile well before the age of fledging. Second, chick behavior and alloparental care in these species are very similar to those in precocial birds. Although adoption can be found in other altricial species, such as storks (Redondo et al. 1995), raptors (Stewart 1981; Bustamante & Hiraldo 1990; Ferrer 1993; Donázar et al. 1991; Simmons 1992; Tella et al. 1997), owls (Roulin 1999), swallows (Beecher et al. 1981), bluebirds (Plissner & Gowaty 1988; Meek & Robertson 1991), warblers (Stutchbury & Ogden 1996), tits (Chauvin 1990), and corvids (Balda & Balda 1978; Baglione et al. 1994), it appears only close to fledging, when the chicks become mobile. Fledging in most altricial species coincides with the termination of parental care, therefore, the fitness costs and benefits of adoption for parents and foster young in these species are probably very different from those in precocial species. ‘True’ adoptions are more likely in precocial birds (Pierotti 1988) (**Table 2.**).

Here I review the hypotheses proposed to explain adoption and brood amalgamation in precocial birds and present a general evolutionary framework for these hypotheses in major groups of precocial birds. The hypotheses based on direct fitness costs and benefits will be discussed first, then I will review sociobiological hypotheses that require more complex approaches to be tested (e.g. molecular studies, modeling).

1.2. THEORETICAL FRAMEWORK: HYPOTHESES AND PREDICTIONS

1.2.1. Cost-benefit hypotheses

In a discussion of the evolutionary significance of any behavior, it is important to distinguish between evolutionary origin (the initial appearance and spread of the behavior) and current utility (the current maintenance and potential modifications in the behavior) (Emlen et al. 1991). This is because in most cases the inferences about the origin of a behavior are limited by the fact that the costs or the benefits of a behavior can be judged only under the current conditions. In this review, I will discuss the hypotheses put forward to explain the maintenance of adoption and brood amalgamation at the current levels. I will address the adaptive value of adoption and brood amalgamation first by discussing costs and benefits for both the alloparent and the foster chick, and will not specifically consider costs or benefits for donor parents or chicks remaining in the natal brood.

The ultimate currency of any behavior is lifetime reproductive success (LRS). In most cases, however, LRS is difficult to assess, therefore, for the purposes of this review, I will consider annual breeding success as the currency for adults. The annual breeding success of adopting adults is a function of the survival of the adults’ own young (resident chicks and genetic chicks that may have been adopted elsewhere; for simplicity, chicks via alternative reproductive strategies will not be considered here). Thus, mechanisms that increase the survival of resident chicks will also increase the annual breeding success and LRS of adopting parents. The fitness costs and benefits of alloparents will be evaluated in relation to the fitness of adults raising only their own genetic young. Similarly, the fitness costs and benefits of foster chicks will be compared to the fitness of chicks reared by their genetic parents. The currency for chicks are chances of survival to fledging (fledging success) *per se*, and survival until breeding and ultimately, LRS. In this review, I will consider fledging success as the currency for the foster chicks.

Because adoption or brood amalgamation may be either selectively beneficial, indifferent or costly for either the alloparent or the foster chick, nine (3x3) logical groups of hypotheses can be envisioned. Scenarios for direct fitness costs and benefits and the mechanisms through which they manifest are shown in **Table 3**. It is important to note that several other conflicts are possible in the case of adoption (e.g. between donor parents and adopting parents, between adopted chicks and resident chicks), however, in this review, I will only address the relationship between the fitness of adopting adults and adopted chicks.

Adoption or brood amalgamation can be adaptive if it is beneficial for at least one of the participants (see explanations in the first row and first column of **Table 3.**). In cases when adoption is either indifferent or costly for both the adopter and adoptee, non-adaptive hypotheses need be considered (see underlined explanations in **Table 3.**). It is important to note that the hypotheses illustrated in **Table 3.** frequently are not mutually exclusive, and several hypotheses can be corroborated in any given species. Therefore, it is recommended to consider all potential explanations at the same time and test those hypotheses that are judged relevant based on the natural history of the species.

1.2.2. Adaptive hypotheses

1.2.2.1. Mutual benefit hypotheses

<u>Detection of predators</u>: Larger broods are better able to detect predators than are smaller broods.

In many precocial species, the detection of predators is very important to avoid predation on chicks, and parental vigilance comprises a large part of the parental effort. If chicks participate in vigilance, a larger brood may be advantageous because the alloparent can spend less time being vigilant, and more time feeding or in self-maintenance (Gorman & Milne 1972). In addition, larger broods may be more efficient at detecting predators than are smaller ones because more individuals participate in vigilance (Kear 1970). A further benefit for individual chicks is that the amount of time each chick spends being vigilant is presumably lower in larger broods than it is in smaller ones.

<u>Defense against predators</u>: Larger broods are better at defending themselves against predators than are smaller broods.

Large broods can be more effective at anti-predator defense than smaller broods because large groups of chicks may confuse and disrupt predator attacks (Gorman & Milne 1972; Lanctot et al. 1995). If chicks participate in the defense against predators, it can be advantageous for an adult to have a larger brood because the protection of its own chicks may be more efficient. To be part of a larger brood may also be beneficial for foster chicks because they may receive a more efficient protection from predators than they would in their natal broods (Gorman & Milne 1972).

Dilution effect: Foster chicks decrease their chance of being preyed upon by joining broods larger than their natal brood. Resident chicks also benefit because their chance of being preyed upon decreases.

This hypothesis predicts that chicks ‘choose’ alien broods which are larger than their own to decrease their chances of being preyed upon (Nastase & Sherry 1997). The adopting adult also must benefit from adoption because the chance that one of its own chicks gets preyed upon decreases (Pierotti 1991). This hypothesis assumes that there is no relationship between brood size and detectability of the brood by predators. Another assumption of the dilution-effect hypothesis is that the predation rates for foster and resident chicks are equal (Kehoe 1989). This hypothesis has been supported by a few studies on waterfowl (e.g. Munro & Bedard 1977a).

Enhanced dominance of larger broods: Adults with larger broods are dominant over adults with smaller broods and larger broods have access to a higher quality or quantity of resources than do smaller broods.

The dominance of a brood may increase with brood size if chicks influence the outcome of conflicts between broods either actively (by assisting adults) or passively (motivating the parents by their numbers). Brood size may be an honest signal for the competitive ability of the parent (Black & Owen 1989a). If there is interbrood competition for resources, a larger, more dominant brood is likely to have access to better, or more, resources than smaller and less dominant broods have (Kehoe 1989; Williams 1994; Loonen et al. 1999). Being part of a larger brood also may be beneficial for the foster chick, because it would gain access to resources to which it probably would not have access in its natal brood. If brood integrity in maintained long after fledging, the enhanced dominance also may be important in wintering areas (Gregoire & Ankney 1990).

Heat conservation: The heat loss of chicks is lower in larger broods than in smaller ones.

Aggregations of individuals may result from their tendency to minimize heat loss to the ambient thermal environment by positioning themselves next to another individual. Thus, it may be advantageous for chicks to aggregate during cold air temperatures (e.g. at night) to conserve heat. In general, larger broods should be better at minimizing heat loss than are small broods (Gorman & Milne 1972; Warhurst & Bookhout 1983; Evans 1984; Carter & Hobson 1988; Kehoe 1989). However, the number of young parents can brood at the same time may limit the size of the brood, and heat loss may be high above a certain brood size.

1.2.2.2. Chick benefit hypotheses

Chick salvage strategy: Chicks abandoned by their genetic parents or expelled by their siblings attempt to gain adoption into foster broods to increase their survival.

When energetically stressed, parents may be limited in their ability to rear their young, and they may be forced to leave their offspring to save their own lives and any future chances for reproduction. If the abandoned young can not survive on their own, there may be selection on deserted chicks to join an alien brood to make the best of a bad situation (Bustnes & Erikstad 1991; Eadie & Lyon 1998). Similarly, chicks expelled from their natal nest by their more dominant siblings may seek adoption into another brood (Roberts & Hatch 1994). Unless adoption or brood amalgamation is costly for adults, chicks should be able to increase their chance of survival by becoming adopted.

Access to resources that are not limiting to the foster brood: Foster chicks attempt to integrate into broods in which they have access to better or more resources than they would in their natal brood.

Chicks can increase their chances of survival by leaving their natal brood if the parental care, or the resources available to them, in the foster brood are of higher quality and/or quantity than those available in their natal brood (Nastase & Sherry 1997). The resources important in the choice of chicks can be food, protective cover against predators, etc. If there is no intrabrood competition for these resources (i.e., they are not limiting the growth of chicks), the foster chicks should not influence the quality or quantity of resources available for the foster parents' own chicks. Therefore, adoption should tend to be indifferent for adopting adults. On the other hand, if resources, or parental care, are limited, and there is intrabrood competition, the conflict between the foster and resident chicks should lead to conflict between the foster chicks and the adopting adults (Pierotti & Murphy 1987).

Mutual attraction of chicks: Adoption and brood amalgamation is the result of a mutual attraction between resident and foster chicks.

The mutual attraction between gregarious chicks could result in a mixing of two or more broods (Williams 1974; Schmutz et al. 1982). Such an attraction can be advantageous to chicks if exhausted parents decide to desert their broods or not based upon the size of their brood (Eadie & Lyon 1998; Pöysa & Milonoff 1999). In such a situation, resident chicks may 'cooperate' with adopted chicks to avoid being deserted by the parent (Eadie & Lyon 1998).

Intergenerational conflict: Disadvantaged chicks, that are younger and/or smaller than their siblings, are selected to leave their natal brood and seek adoption by, and solicit alloparental care from, unrelated parents which can not discriminate among chicks.

This hypothesis predicts that chicks that are subordinate to their siblings, and/or receive inadequate parental care in their own brood, are more likely to depart from their natal brood and seek adoptions elsewhere than would be their more dominant siblings (Graves & Whiten 1980; Pierotti & Murphy 1987; Hébert 1988). If these adoption-seeking chicks can hinder a foster parent's ability to recognize its own young, they can get established in the foster brood (Pierotti & Murphy 1987). On the other hand, if parental investment and/or the resources are limited, alloparental care should dilute investment in resident chicks, and will decrease the survival of resident chicks. Therefore, adoption involves fitness costs for adults because their breeding success decreases (Pierotti & Murphy 1987). Behavioral constraints, for example, a foster parent's inability to recognize its own chicks, may make foster parents unable to avoid these costs. This lack of recognition could result from the high costs of evolving chick recognition or the high costs of a recognition error (rejecting genetic offspring) (Knudsen & Evans 1986; Pierotti & Murphy 1987). Thus, any asymmetry in fitness benefits and costs for chicks and parents will largely determine who 'wins' the intergenerational conflict (Pierotti 1991). This hypothesis is analogous to Eadie et al.'s (1988) 'constraint' hypothesis and its predictions are similar to those of Mock's (1984) 'posthatch brood parasitism by vagrant chicks' hypothesis, to Hébert's (1988) 'runaway chicks' hypothesis, and Brown's (1998) 'chick tactic' hypothesis. Most studies of adoption in gulls and terns support at least one prediction of this hypothesis.

Heat gain during brooding: The foster chick may receive more heat during brooding bouts than resident chicks do if it is located under the brooding parent in a position more central than the position of the resident chicks.

Weather can be an important source of chick mortality for some precocial species. In such species the positioning of chicks during brooding may influence the warmth they receive from the parent and, therefore, it may enhance survival. For example, murre chicks often solicit brooding from alloparents when unattended by their genetic parents (Birkhead & Nettleship 1984). Furthermore, Warhurst & Bookhout (1983) observed that young Canada Geese (*Branta canadensis*) were not brooded but huddled together beside the female, and in such cases, the resident chicks may 'insulate' the foster chicks. The same study found higher survival rates for foster chicks than for resident chicks (Warhurst & Bookhout 1983), however, the relationship between brooding and survival remained unclear.

1.2.2.3. Adult benefit hypotheses

Adult parenting experience: Adoption of alien chicks provides an opportunity for inexperienced breeders to gain knowledge/expertise in raising chicks.

If adopters are either adults that failed in an earlier phase of breeding or subadults, it is possible that by caring for young other than their own may increase their chances of a successful breeding in the future at no direct costs ('of experimenting') for them (Riedman 1982). This hypothesis predicts that adopting adults are first-time or inexperienced breeders and/or that they may be previously failed breeders (Munro & Bedard 1977b; Schmutz et al. 1982).

Adult attraction: Brood amalgamation is a result of mutual attraction among adults with broods or among adults with broods and failed breeders.

This hypothesis suggests that brood amalgamation is simply a result of the gregarious nature of breeding adults (Schmutz et al. 1982). This may be advantageous for adults if the physiological costs of brood rearing are reduced by minimizing stress in large groups that are considered "safe" by adults. Adults without broods (failed breeders) also may be attracted to broods during searching for future nesting sites (Schmutz et al. 1982).

Signal for adult quality: Brood size is positively related to adult quality and may serve as a signal for adult quality.

More experienced, or more dominant, birds may use brood size as an honest signal to demonstrate their parental abilities. This signal may be important in mate choice by the opposite sex. Ducklings have been observed to aggregate behind the most aggressive, most stimulating, 'superbroody' females in several species (Kehoe 1989).

Diluting effect: Adults decrease the chance that their own chicks are preyed upon by increasing the size of their brood through adoption or brood amalgamation.

This hypothesis predicts that the chance that an adult’s own young is preyed upon decreases with increasing brood size. Thus, adults should actively solicit young of alien adults. The hypothesis assumes that the survival of alien chicks is similar to that of their siblings remaining in the natal brood. It also assumes that there is no positive relationship between brood size and detectability of the brood by predators (Munro & Bedard 1977a). In contrast to the mutually beneficial ‘dilution effect’ hypothesis, this hypothesis predicts that predation rates are higher for foster than for resident chicks, therefore, adoption is beneficial for the foster parent (Kehoe 1989).

Exploitation of foster young through a selfish herd effect: Adults decrease the chance that their own chicks are preyed upon by increasing the size of their brood, and the survival of foster chicks is lower in the foster brood than in their natal brood.

This hypothesis is similar to the ‘Diluting effect’ hypothesis; the only difference being is that the survival of foster chicks decreases by adoption or brood amalgamation. This is possible if foster chicks are more vulnerable to predation are than resident chicks because of either their lower dominance or more peripheral position in the brood, their inappropriate reaction to the foster parent or their being further away from the adults (Nastase & Sherry 1997). Alternatively, foster chicks may have weaker ties to, or may even be attacked by, the foster parent (Kear 1970) or the resident chicks. Thus, foster chicks may follow the brood at a greater distance, which makes them more likely to be taken by predators (Larsson et al. 1995; Nastase & Sherry 1997). Thus, the adopting adults may protect their chicks by using the foster chicks as ‘living shields’ against predators. This effect may be especially important in species in which predation is the main cause of mortality (Eadie et al. 1988; Kehoe 1989; Pierotti 1991).

Exploitation of foster chick during brooding: The resident chicks may receive more warmth during brooding bouts than do foster chicks if resident chicks are located under the brooding parent in a more central position than are the foster chicks.

If weather causes chick mortality, the amount of heat the parents can transfer to their young during brooding may be important. The positioning of chicks in relation to the brood patch of the parent may influence the amount of heat they receive, and therefore, it may be related to their survival. If the foster chicks follow parents at a greater distance than do the resident chicks (Larsson et al. 1995; Nastase & Sherry 1997), they may reach the brooding parent later, and therefore, they may be forced to the side and thus may 'insulate' the resident chicks.

1.2.3. Non-adaptive hypotheses

Neutralism: Adoption or brood amalgamation is simply a result of accidental mixing of broods and does not influence either the breeding success of adults or the fledging success of chicks.

The neutralism hypothesis predicts that neither the costs nor the benefits of either participant are significantly different from zero. According to this hypothesis adoption or brood amalgamation happens by chance alone, and there is no selection for or against it. This explanation is analogous with the 'accidental brood-mixing' hypothesis proposed by several authors (Williams 1974; Patterson et al. 1982; Savard 1987; Savard et al. 1998).

Indirect selection: Adoption may be positively correlated to traits which are favored by selection, therefore, adoption may evolve by indirect selection.

The high frequency of adoption in some taxa may be maintained indirectly if selection favors a trait that is genetically or phenotypically correlated with adoption (Avital & Jablonka 1996). Two conditions are necessary for this (Hansen 1996). First, individuals showing the adopting trait and the trait positively correlated with it should be able to rear more offspring than non-adopters, and second, adopted offspring or their siblings should be likely to be adopters (Hansen 1996).

Side effect of territoriality: Brood amalgamation is a side-effect of competition for territories between brood-rearing adults. The winners of territorial conflicts adopt the young of evicted parents.

Under crowded conditions, territories may not be available for all broods. In such cases the adult, or mated pair, winning territorial conflicts may evict the loser. The chicks of the loser may not be able to follow their evicted parent and may become amalgamated in the brood of the winner. Thus, brood amalgamation may be an accidental outcome of territorial aggression (Savard 1987). This hypothesis has been supported by several studies of brood amalgamation in waterfowl (Williams 1974; Titman & Lowther 1975; Savard 1987; Mitchell & Rotella 1997).

Adult error: Adoption or brood amalgamation occurs as an error (e.g. in chick recognition) on the side of the adult.

This hypothesis predicts that even though adoption is costly for adults, at the time of adoption the parents are unable to recognize their own chicks and/or do not discriminate between their own and alien chicks. In other words, chick recognition may develop at a time later than when parents are exposed to chicks seeking adoptions (Tinbergen 1953; Roberts & Hatch 1994; Brown 1998). Adoption should be neutral to the foster chick based on this hypothesis.

Chick error: Adoption or brood amalgamation occurs as an error (e.g. in parent recognition) on the side of the chick.

This hypothesis states that even though being adopted is costly for a chick, chicks do not recognize their parents and/or are not be able to stay in their own brood. For example, chicks may be unable to follow their parents during brood movement. Thus, chicks get lost and may join alien broods by which their survival decreases.

Maladaptation: Adoption, or brood amalgamation, is the result of conditions that have not existed long enough for selection to act on the behavior.

An example for this hypothesis comes from colonial nesters that breed in densities higher than their usual density as a result of habitat loss or some other factor. In such super-dense colonies, adoption rates may be high even though adoption involves costs to both adults and chicks (Holley 1981, 1984; Carter & Spear 1986; Saino et al. 1994). Another example may be if larger broods are more likely to be detected by predators than are smaller broods, the success of both participants will be lower than that of individuals not involved in adoption.

1.2.4. Sociobiological hypotheses

Kin selection: Because the foster parent and the adopted chicks are related, adoption or brood amalgamation increases the inclusive fitness of the foster parent and the fitness of the adopted young.

Hamilton’s (1964) principle predicts that an altruistic behavior can be adaptive if the degree of relatedness between the donor and acceptor of the altruistic behavior exceeds a certain level. If the degree of relatedness between the foster parent and foster chick is high enough, the direct costs of adoption may be outweighed by the indirect fitness gains arising from genetic relatedness. Such a mechanism can work in kin groups. Philopatry, for example, is thought to increase the likelihood of forming kin selection (Kehoe 1989). If such a pattern exists, adoption is likely to take place between relatives, thus, it may be favored by selection.

Reciprocal altruism: Even though adoption or brood amalgamation involves proximate costs for the foster parent, the benefits to the genetic parents are higher than are the costs for the foster parent, and adults reciprocate the altruistic behavior.

An altruistic behavior can be maintained in the population if selfish individuals return the favor of other, previously altruistic, individuals at a later time (Trivers 1971). In other words, some individuals may adopt at a given breeding attempt and they may desert or lose chicks to adoption at another attempt. Such a strategy can exist only if the probability of finding adults capable of returning similar help is high enough (Axelrod & Hamilton 1981). One assumption of reciprocity is that the costs to the adopter parent should not exceed the benefits to the donor parent (Brown

1998). Another prediction is that individuals change roles between breeding attempts, for example, younger and inexperienced breeders may lose chicks to adoption whereas older and more experienced breeders may adopt their chicks (Pierotti & Murphy 1987; Eadie et al. 1988; Kehoe 1989).

Transfer of socially learned information: Adoption or brood amalgamation is a route for foster parents to transfer learned information to the next generation through the social learning of behavior patterns by young.

Socially learned behavior, including parenting styles, can be transferred through generations independently from genetic inheritance through social learning (Avital & Jablonka 1994). If foster parents accept unrelated young, they may do so to ‘teach’ them certain behaviors. Thus, if the behavioral transmission increases the representation of the ‘adopting’ phenotype in future generations, the adopting phenotype can be maintained in the population even in the lack of a direct link between adoption or brood amalgamation and fitness costs or benefits.

Matchmaking hypothesis: Foster parents accept unrelated young that potentially can be future mates for their genetic young.

Adoption or brood amalgamation may provide benefits by leading to an “arranged marriage” between the foster parent’s genetic young and an unrelated young, i.e., parents provide their genetic young with future unrelated mates by adopting foreign young (Avital et al. 1998). Characters of species for which this may be important include biparental care, mating for life, and brood amalgamation.

1.3. The adaptive significance of adoption and brood amalgamation in precocial birds

Here I review the conclusions of studies that have tested hypotheses about the adaptive significance of adoption and brood amalgamation in precocial species (**Table 2.**).

1.3.1. Rheas (order *Struthioniformes*, family *Rheidae*)

Two studies, one observational and one semi-experimental have investigated the adoption behavior in rheas. Codenotti & Alvarez (1998) found that in the Greater Rhea (*Rhea americana*) 23% of broods contain adopted chicks. Foster chicks are usually younger than resident chicks, thus, the exploitation of foster chicks through a dilution or selfish herd effect was possible. However, adopted chicks have a higher short-term survival than resident chicks in adopting broods, whereas there is no difference in long-term survival between these two types of chicks (Codenotti & Alvarez 1998). Artificial adoption experiments by Lábaque et al. (1999) have also shown that the survival of foster and resident chicks is not different.

Adopting males (the primary caregivers in rheas) spend more time vigilant, brood chicks more frequently and are more aggressive to conspecifics than are non-adopting males (Codenotti & Alvarez 1998). This may indicate either that adopters can be superior parents or that adoption involves some behavioral costs for the adopters. Codenotti & Alvarez (1998) posit that young may choose superior parents. Adult quality is also thought to be an important confounding factor in artificial adoptions (Lábaque et al. 1999). Adopting parents can derive long-term benefits of larger brood sizes, which may be important in determining the hierarchy of males in wintering flocks or in the choice of females during later breeding attempts (Codenotti & Alvarez 1998). In conclusion, adoption has been shown to be beneficial for the foster chicks, and the asymmetry between the fitness costs to the adult and benefits to the foster young appears to determine the outcome of the intergenerational conflict toward the success of chicks seeking adoption into alien broods (Codenotti & Alvarez 1998).

1.3.2. Grouse and turkeys (order *Galliformes*, family *Phasianidae*)

Two cases of adoption have been reported in the Ruffed Grouse (*Bonasa umbellus*) (Maxson 1978) and four cases in Merriam's Wild Turkey (*Meleagris gallopavo merriam*). There are no data available on the potential fitness costs or benefits. Costs may involve increased competition among chicks if food is limited, whereas benefits may include increased probability of predator detection and decreased chance of being predated for the adopter's own chicks (Maxson 1978; Mills & Rumble 1991). Adoption and brood amalgamation is probably more widespread in this clade (Pierotti 1988) and anecdotal observations support this claim (e.g. Johnsgard 1983).

1.3.3. Ducks and geese (order *Anseriformes*, family *Anatidae*)

A review of North American waterfowl found that post-hatch brood amalgamation has been reported in 28 species (Eadie et al. 1988). Later, evidence for brood amalgamation has been reported in 47 (29%) of 162 species of waterfowl (Beauchamp 1997). In waterfowl there is a continuum from pre-hatch clutch parasitism to post-hatch brood amalgamation and the two processes should be treated together (Eadie et al. 1988). A comparative study supports this idea because evolutionary transitions to post-hatch brood amalgamation occur most often in lineages that also carry the pre-hatch clutch amalgamation character state (Beauchamp 1997). Furthermore, the presence of pre-hatch brood amalgamation appears to be related to the occurrence of colonial breeding and cavity nesting in lineages (Beauchamp 1997). In North American *Anatidae* the occurrence of brood amalgamation was associated with low relative resource availability, delayed maturity, small clutch size and body mass, long-term pair-bonds and biparental care (Eadie et al. 1988). Since the first theoretical framework was proposed for the hypotheses on brood amalgamation in waterfowl (Eadie et al. 1988), several studies have been published that bear on these and other hypotheses.

1.3.3.1. Natural history of adoption and brood amalgamation in Anatidae

In ducks and geese of the family *Anatidae*, adults lead their young away from the nest to feeding areas. Adoptions and brood amalgamations usually form in two ways after the broods leave the nest. First, adoption and brood amalgamation may occur during the joint movement of several broods. For example, in the Common Eider (*Somateria mollissima*), several chicks simply follow unrelated adults when broods encounter one another in areas of high brood density (Gorman & Milne 1972). Brood amalgamations also appear to be associated with brood movements in the Trumpeter Swan (*Cygnus buccinator*) (Mitchell & Rotella 1997). Second, adoption and brood amalgamation also may occur after the broods reach the feeding sites. Brood encounters in these areas can also result in one or more chicks switching broods. For example, in Canada Geese goslings become separated from their natal family during feeding and may be adopted into other families (Zicus 1981). In the Shelduck (*Tadorna tadorna*), females desert their broods as soon as they reach the feeding areas and the amalgamation of broods coincides with the overcrowding of nursery areas (Hori 1964). Females remaining with amalgamated broods are those that reach the feeding area first (Hori 1969).

The frequency of brood amalgamation and adoption can be high in some species. For example, in Canada Geese the proportion of broods involved in either amalgamation or adoption was as high as 74% in one study (Warhurst & Bookhout 1983), and 62% in another (Nastase & Sherry 1997). In Common Eiders, 47% of ducklings were in a brood other than their natal brood (Bustnes & Erikstad 1991), and between 25% and 38% of broods contained adopted young in another study (Öst 1999). The annual proportion of broods involved in amalgamation was 38% in Barrow's Goldeneye (*Bucephala islandica*) and 34% in the Bufflehead (*Bucephala albeola*) (Savard 1987), and 26% in the Surf Scoter (*Melanitta perspicillata*) (Savard et al. 1998).

It is important to emphasize that the frequency of brood amalgamation and adoption reported by most studies are likely underestimates. This is because usually only a portion of the breeding population is marked, and the transfer of unmarked chicks are likely underdetected (e.g. in the Trumpeter Swan, Mitchell & Rotella 1997).

Adoptions and brood amalgamations can now be detected indirectly by assessing the relatedness of chicks and adults using multilocus DNA-fingerprinting. In waterfowl, three studies have applied molecular, DNA-based techniques to detect adoptions; one study was conducted in the Mute Swan (*Cygnus olor*) and two in the Barnacle Goose (*Branta leucopsis*). In Mute Swans, an unusually large brood was shown to be composed of nine genetic young and six full siblings unrelated to the resident brood (Meng & Parkin 1991). Based on band-sharing coefficients Choudhury et al. (1993) detected one adopted gosling in a sample of 35 chicks in Barnacle Geese. Field observations in this species suggested that the proportion of adopted goslings ranged from 6% in one year to 25% in another and that 13 and 24% of the broods contained adopted goslings (Choudhury et al. 1993). Larsson et al. (1995) found that 17% of goslings (n = 137) were extra-pair (adopted) chicks and 27% of families (n = 63) contained adopted goslings. However, the latter study could not differentiate whether alien young got into the brood before hatching (brood parasitism) or after hatching (adoption).

Direct observations on how chicks get from one brood into another suggest several important cues as to the fitness costs and benefits for the foster parent. Adults of species in which adoption or brood amalgamation incurs net costs for the foster parent should be able to reject alien chicks. However, in most waterfowl species, no aggression by adults against alien chicks has been reported. For example, goslings can intermingle freely among broods and adults pay little attention to which and how many goslings they attend in the giant Canada Goose (*Branta canadensis maxima*) (Seddon & Nudds 1994). In other species, parents reportedly first behave aggressively toward alien goslings, but eventually accept them, for example, in the Shelduck (*Tadorna tadorna*) (Williams 1974), and in the Bufflehead (Savard 1987). In Barrow's Goldeneye, adults have been observed to behave aggressively toward, and even kill alien young (Savard 1987). To my knowledge, aggression by parents resulting in killing of the alien young has not been reported in other species of waterfowl.

1.3.3.2. Mutual benefits for adults and young in Anatidae

Several studies have found advantages of adoption and brood amalgamation in waterfowl. In geese, brood size and dominance are related and the dominance status of individuals is determined by the size of their brood (White-fronted Goose (*Anser albifrons albifrons*): Boyd 1953; Shelduck (*Tadorna tadorna*): Hori 1964; Canada Goose: Raveling 1970; Nastase & Sherry 1997; Pink-footed Goose (*Anser brachyrhynchus*): Lazarus & Inglis 1978; Bar-headed Goose (*Anser indicus*): Schindler & Lamprecht 1987; Barnacle Goose: Black & Owen 1989a; Loonen et al. 1999; Lesser Snow Goose (*Chen caerulescens caerulescens*): Williams 1994). Larger broods may be dominant over smaller broods for several reasons. First, adults with larger broods may have a higher number of assistants in conflicts. Brood members participate in unified action during aggressive brood encounters in wintering Canada Geese (Raveling 1970). Second, in larger broods a higher number of vigilant individuals can monitor the behavior of neighbors (Black & Owen 1989a). Finally, brood size also may be positively correlated with adult quality (Black & Owen 1989a; Williams et al. 1994). In Barnacle Geese, parents with larger broods spend more time engaged in aggressive behavior, and aggression rate is positively related to age (Black & Owen 1989a). Thus, it is likely that adults with larger broods are older and more experienced. Adult quality, therefore, also may explain the relationship between brood size and dominance.

However, experimental evidence indicates that dominance is directly related to brood size, and therefore, brood size may be an honest signal for competitive ability and dominance in the Barnacle Goose (Loonen et al. 1999). Goslings were thought to increase the aggressiveness of adults and initiators of aggression are usually the winners of conflicts in this species (Loonen et al. 1999). The body mass of adult females has been shown to be positively correlated with brood size, suggesting that aggression involves small costs or no costs for females and that adults benefit from larger broods (Loonen et al. 1999).

The relationship between brood size and dominance, however, is generally more complex. For example, dominant male Shelducks lost chicks to adoption rather than gained them because dominant males are more aggressive than are less dominant ones and males tend to lose chicks to other adults during fights in this species (Patterson et al. 1982).

A benefit of higher dominance in *Anatidae* is that broods of more dominant parents can gain access to more resources or resources of higher quality than broods of subordinate parents (Raveling 1970; Kehoe 1989). For example, in the barnacle goose larger and more dominant broods have the first choice of plants and spend more time in areas of higher grass biomass than do smaller broods (Black & Owen 1989a). Large broods in this species also have been found to use more feeding space than small broods (Loonen et al. 1999). The home range of Common Eider is correlated positively with brood size, indicating that larger broods tend to use a larger feeding area (Öst & Kilpi 2000).

Larger broods may benefit from their dominance only when there is interbrood competition for feeding sites (Loonen et al. 1999). If there is no such competition, brood size may not influence the access to resources, and this may explain why the feeding time of chicks in some species does not correlate with brood size (e.g. in giant Canada geese, Seddon & Nudds 1994).

It is likely that access to more, or higher quality, resources translates into a faster growth of chicks. Goslings in larger broods grow faster than do goslings in smaller broods in the Lesser Snow Goose (Cooch et al. 1991). In barnacle geese the growth rate of goslings, measured after the age of 30 days, increased when brood size was experimentally increased, and growth rate decreased when brood size was decreased (Loonen et al. 1999). Because growth rate is positively correlated with adult body size, gosling growth rate can be related to a number of life history traits (Cooch et al. 1991).

Another benefit of larger broods in waterfowl can be the dilution of predation. Chick mortality by predation by single gulls decreases with increasing brood size in Common Eider (Munro & Bedard 1977a). Even though predation by groups of gulls is likely to lead to the complete loss of the brood, the overall mortality of ducklings decreases with brood size (Munro & Bedard 1977a). Thus, there is a survival advantage for ducklings in larger broods over those in smaller broods (Munro & Bedard 1977a). This effect also has been thought to be important in White-winged Scoters during the early part of brood rearing, the most vulnerable period of the ducklings' life (Kehoe 1989).

Other potential benefits that correlate positively with larger broods over longer time periods include higher dominance of broods on the wintering grounds (Barnacle Goose: Black & Owen 1989b; Lesser Snow Goose Gregoire & Ankney 1990; Williams 1994), increased overwinter survival of adults (Emperor Goose (*Chen canagica*): Petersen 1992), larger clutch size the following year (Lesser Snow Goose: Williams et al. 1994), and higher number of young wintering the following year (Barnacle Goose: Black & Owen 1989b).

1.3.3.3. Benefits for chicks

Several studies of waterfowl supported the view that gaining adoption is a salvage strategy of chicks deserted by their parents (Hori 1964, 1969; Ahlén & Andersson 1970; Gorman & Milne 1972; Bustnes & Erikstad 1991; Afton & Paulus 1992; Eadie & Lyon 1998). The factors influencing the decision of adults to desert young are difficult to separate and have been the subject of debate (Pöysa 1995; Bustnes & Erikstad 1995; Eadie & Lyon 1998; Pöysa & Milonoff 1999).

First, energetic stress may limit parents in their ability to rear their young (Ahlén & Andersson 1970; Gorman & Milne 1972; Bustnes & Erikstad 1991) and may force them to desert their young to meet their own energetic needs. For example, Common Eider females do not feed during incubation, therefore, these parents need to feed as soon as possible after hatching occurs if they are to survive (Gorman & Milne 1972). Thus, females in poor body condition more frequently desert their young soon after hatching, whereas females in good body condition tend to rear their young and even adopt alien young (Erikstad et al. 1993). Such a trade-off between allocating time and energy to survival versus brood rearing has been considered to be important in several other studies (Bustnes & Erikstad 1991; Erikstad et al. 1993; Öst 1999).

Second, exhausted parents may assess the chances of successfully rearing their chicks by the number of chicks in their brood, and they may desert their brood to save some investment for future reproduction (Pöysa 1995; Eadie & Lyon 1998). The size of the brood has been thought to be the proximate factor in this decision. Eadie & Lyon (1998) have provided experimental evidence that female Barrow’s Goldeneye (*Bucephala islandica*) base their decision to desert or not on the number of their offspring. Females with experimentally reduced broods are more likely to desert young than controls and broods containing fewer than 4-6 ducklings are more likely to be deserted than broods containing more ducklings (Eadie & Lyon 1998). These results, however, have been questioned on the grounds that duckling mortality could not be tracked to the act of desertion (Pöysa & Milonoff 1999). If chick mortality occurred before abandonment, the proximate cause of desertion may be low chick survival rather than the size of the brood (Pöysa & Milonoff 1999).

Finally, chick survival can provide clues to females as to the chances of successful reproduction, and if chick survival is low due to high mortality early in the brood-rearing period, they may desert their brood (Carlisle 1982; Pöysa 1995; Pöysa & Milonoff 1999). Low survival of chicks, therefore, may be the proximate factor in desertion (Pöysa 1995). The mortality rate of Common Goldeneye (*Bucephala clangula*) ducklings has been found to influence the time when desertions occurred (Pöysa 1992).

Deserted young usually have lower survival than do young reared by their own parents (Bustnes & Erikstad 1991; Eadie & Lyon 1998), suggesting fitness costs of being deserted. Because ducklings require protection by adults for their survival, they may have no other option but to join other broods. Increase in brood size of Common Eider due to adoption did not lead to greater parental effort or duckling survival, suggesting that adoption may be of neutral value to parents and their chicks (Bustnes & Erikstad 1991). Similarly, fledging success did not differ between adopting and non-adopting broods in Barrow's Goldeneye (Eadie & Lyon 1998). Therefore, adoption may be neutral, even though females initially behave aggressively against alien young in this species (Savard 1987; Eadie & Lyon 1998).

Chicks may benefit from brood amalgamation beyond simply assuring their survival. In the White-winged Scoter (*Melanitta fusca deglandi*) amalgamated broods result from an apparently random assembly of ducklings, and duckling survival is higher in larger broods than in smaller broods (Kehoe 1989). Even though some females tend broods that do not contain any of their own young, brood amalgamation does not involve energetic costs for females, thus, it has been concluded neutral for females (Kehoe 1989).

Giant Canada Goose young have been shown to wander from their own brood and gain adoptions into alien broods during the first two weeks of their life (Warhurst & Bookhout 1983), probably because they are not imprinted on their parents at this early age. The goslings are thought to benefit from a better thermoregulation in large groups (Warhurst & Bookhout 1983). The survival rate of adopted goslings was 90% (n = 103), and for all other goslings it was 74% (n = 182) (Warhurst & Bookhout 1983, pp. 1120, 1123). The authors did not compare these proportions, which, interestingly, are significantly different (Yates corrected $\chi^2 = 9.69$, df = 1, p = 0.0019). Therefore, adopted goslings survived in higher proportions than did other chicks. However, the mechanism for this pattern remains unclear.

1.3.3.4. Benefits for adults

Adults may benefit from larger broods in several ways. First of all, brood size may serve as a signal for parental abilities, which may be important in future reproduction attempts. Koskimies (1955) reported that predation, or chance encounters, alone do not necessarily lead to the formation of brood amalgamations, but that the effect of a ‘superbroody’ female is also important for brood amalgamation in the Velvet Scoter (*Melanitta fusca*). Similarly, ducklings tend to cluster behind the most broody (most stimulating) female in Common Eiders (Ahlén & Andersson 1970; Munro & Bedard 1977b), in the Common Merganser (*Mergus merganser*) and in the Red-breasted Merganser (*Mergus serrator*) (Bergman 1956). Characters that probably stimulate ducklings are vocalization, posture, and aggression towards other females. It is not clear whether ducklings benefit from being tended by a more vigorous female, or whether brood size is in fact associated with higher chances of successful breeding in the future for the foster parent.

Secondly, foster chicks may be exploited by adults if adopted chicks are more likely to become preyed upon than are resident chicks. For example, the adopted chicks may be farther away from the vigilant parent than are resident chicks. Adopted young in Barnacle Geese were first attacked by parents and followed the brood at a greater distance, and may have been more prone to predation by gulls (Larsson et al. 1995). Alternatively, the ties between foster chicks and foster parents may be weaker, which may make the foster chicks more vulnerable to predation. This might happen in Canada Goose, in which goslings are known to imprint on their parents' alarm calls (Cowan 1973), so the foster chick may be at a disadvantage (Seddon & Nudds 1994).

Long-term benefits of larger broods for adults may include higher overwinter survival and subsequent reproductive success. In lesser snow geese, adopting adults have a higher return rate the following year than non-adopting adults, even though there are no differences in time budgets, age, initial brood size or body condition between adopting and non-adopting adults (Williams 1994).

1.3.3.5. Costs of increased brood size in Anatidae

In birds that do not feed their chicks, parental care has been predicted to be unrelated to brood size because parental care benefits all chicks simultaneously (unshared or non-depreciable care, Lazarus & Inglis 1986; Clutton-Brock 1991). For example, vigilance, which makes up a major part of parental care, is not related to brood size in the Pink-footed Goose (*Anser brachyrhynchus*) (Lazarus & Inglis 1978), and the Lesser Snow Goose (Lessells 1987). Vigilance, however, is positively related to brood size and distance between parents and young in the Barnacle Goose (Forslund 1993). Furthermore, higher predation generally leads to higher vigilance in Barnacle

Geese, and parents decrease vigilance when their brood becomes smaller due to predation (Forslund 1993). In Canada Geese, the positive relationship between vigilance and brood size has been shown to be significant only for males (Sedinger & Raveling 1990). A similar relationship has been found in Black Brant (*Branta bernicla nigricans*), in which the percentage of time spent alert was positively correlated with brood size in males but not in females (Sedinger et al. 1995). In a semi-captive population of Bar-headed Geese (*Anser indicus*) attacks by males on neighboring pairs, and approach of young showed a positive correlation with brood size (Schindler & Lamprecht 1987). These observational studies, however, could not refute the alternative hypothesis that adults of higher adult quality have larger broods. A recent experimental study using randomly manipulated pairs of Barnacle Goose, however, provided evidence that pairs with experimentally enlarged broods were more vigilant than pairs with reduced broods (Loonen et al. 1999).

The time spent being vigilant is negatively correlated with time for feeding in the Barnacle Goose (Black & Owen 1989a). There appears to be a negative relationship between brood size and feeding time in the Lesser Snow Goose, suggesting that increased vigilance may reduce the time available for feeding, and thus, for self-maintenance (Williams et al. 1994).

Several other costs of increasing brood size have been proposed. Larger broods, for example, may be more difficult to defend by parents because young may tend to be more dispersed in larger broods, and the probability of young positioned on the periphery increases with brood size (Sedinger et al. 1995). This may increase parental effort and decrease parental body condition. Alternatively, intrabrood competition may be higher in larger broods than in smaller ones, which could lead to a lower survival of chicks in larger broods.

The costs of rearing experimentally enlarged broods were small in Canada Geese (Lessells 1986). Adult females molted later and their body mass decreased with increasing brood size, and pairs with experimentally enlarged broods nested later the following year (Lessells 1986).

However, brood size did not affect the subsequent survival or reproductive performance of adults (Lessells 1986). Gosling survival and growth rate were not correlated with brood size, and survival decreased only in broods well above the normal range of brood sizes (Lessells 1986). These results illustrate that even though parental condition may decrease with increasing brood size, these changes appear not to lead to measurable changes in parental fitness or chick survival.

Thermoregulatory costs of larger broods have been found in the Common Eider (Öst 1999). The number of ducklings per brooding female increases with the size of the amalgamated brood, and this results in less efficient brooding and a higher exposure of young chicks to chilling (Öst 1999).

The proportion of offspring surviving for 20 days after their initial sighting was lower in larger broods than in smaller broods in the Common Goldeneye (Andersson & Eriksson 1982). However, this relationship also can be attributed to a sampling bias, because larger broods may have been initially sighted at a younger age than were smaller broods, and there is ample evidence that most duckling mortality occurs during early brood rearing (Rohwer 1985).

1.3.3.6. Non-adaptive explanations

Numerous studies found no evidence for costs or benefits of adoption or brood amalgamation and support the view that this behavior is selectively neutral (Williams 1974; Titman & Lowther 1975; Patterson et al. 1982; Warhurst & Bookhout 1983; Bustnes & Erikstad 1991; Gosser & Conover 2000). Several studies supporting neutrality also report that adoptions and brood amalgamations are accidental results of the high density of broods at a given brood-rearing area (Trumpeter Swan: Mitchell & Rotella 1997; Shelduck: Patterson et al. 1982; Common Eider: Gorman & Milne 1972; Munro & Bedard 1977b; Surf Scoter: Savard et al. 1998; Canada Goose: Gosser & Conover 2000).

There is no difference in survival between adults that deserted their brood (donors) and those that reared their amalgamated broods (recipients) in the Shelduck (Patterson et al. 1982). Ducklings in larger broods spend more time with feeding, tend to grow faster and fledge in a shorter time than chicks in smaller broods (Williams 1974). However, the fledging success of chicks tends to be lower in amalgamated broods than in natural broods because of a higher mortality in amalgamated broods immediately after adoption (Williams 1974). Brood amalgamation has been thought to result from the mutual attraction of ducklings toward each other, and the high short-term mortality following it is offset by a higher feeding rate and shorter fledging period in this species (Williams 1974). Brood amalgamation in Shelducks is probably a side effect of the high density of broods in the brood-rearing areas (Williams 1974; Patterson et al. 1982).

Adoption in waterfowl also has been considered to be an abnormality in the territorial system of broods occurring only in situations of extremely high breeding density, for example, in Mallards (*Anas platyrhynchos*) (Titman & Lowther 1975). In giant Canada Geese, brood size affects the time that adults spend vigilant only for males but not for females or both sexes combined, suggesting that adoption has no behavioral costs (Seddon & Nudds 1994). Similarly, goslings in larger broods appear not to benefit from greater foraging opportunities or better predator detection (Seddon & Nudds 1994). The frequency of brood amalgamation in a Connecticut population of Canada Goose was related only to the number of individuals at a site, but not to food availability or predation risk (Gosser & Conover 2000). There were no behavioral or survival costs of tending amalgamated broods in the Lesser Scaup (*Aythya affinis*) and duckling survival also did not differ between single and amalgamated broods (Afton 1993).

An experiment manipulating clutch size in the Blue-winged Teal (*Anas discors*) also supports the neutrality hypothesis (Rohwer 1985). Neither duckling survival nor the body mass of fledglings differed among the experimentally reduced, normal and experimentally enlarged broods (Rohwer 1985). The behavioral costs of brood rearing and the number of young produced did not differ among treatment levels (Rohwer 1985).

Brood amalgamation also can be a side effect of the territorial interactions among broods. Female Barrow's Goldeneye and Bufflehead (*Bucephala albeola*) with broods defend territories in the feeding areas (Savard 1987). Brood encounters involve violent fights between females, and the loser of the fights is often expelled from the lake leaving her young behind. In the beginning the winner chases the alien young but eventually will tolerate them (Savard 1987). Brood size does not influence the survival of ducklings (Savard 1987), therefore, brood amalgamation may be neutral for the adopting females.

Adoption and brood amalgamation also can result from disturbance by humans. For example, under some circumstances human disturbance (the researchers' activity) can be the most important factor influencing the formation of adoptions in the Pink-footed Goose (*Anser brachyrhynchus*) (Lazarus & Inglis 1978). Under such conditions, the increase in brood size does not lead to changes in any aspects of the time budget of parents, but the survival chances of resident and foster chicks remain unknown (Lazarus & Inglis 1978).

Long-term costs or benefits of caring for alien chicks have been found small or absent in Barnacle Geese (Larsson et al. 1995). Subsequent survival and reproductive effort do not differ for adults caring for alien young and those not caring for alien young. Similarly, the subsequent survival and reproductive effort of fledglings is similar, regardless of whether they fledged in their natal or in an alien brood (Larsson et al. 1995), but this study did not evaluate costs or benefits during brood rearing.

1.3.3.7. Sociobiological explanations of brood amalgamation in Anatidae

Kin selection, or reciprocal altruism, is thought to exist in Common Eider nesting on the Baltic Sea, where females from different colonies use spatially segregated brood-rearing areas (Öst & Kilpi 2000). Because brood amalgamations usually take place among females from the same colony, kin selection or reciprocal altruism may explain brood amalgamation (Öst & Kilpi 2000).

Reciprocal altruism also has been thought to exist in Common Eiders, in which two conditions appear to be necessary for such cooperation. First, adoption is of neutral selective value to recipients (Gorman & Milne 1972; Bustnes & Erikstad 1991), therefore, the benefits for donors in terms of salvaging at least some of their reproductive effort outweigh the potential costs to adopters. Second, desertion and adoption are not obligate strategies, but may change from year to year (Bustnes & Erikstad 1991).

An interesting aspect of the social system of Common Eider is the presence of helpers near amalgamated broods. These females are usually failed breeders, with prolactin levels lower than that of breeding females and similar to that of non-breeding males (Schmutz et al. 1982). Thus, the hypothesis that misdirection of parental care results from high hormone levels of failed breeders has been refuted (Schmutz et al. 1982). Alternatively, these females may benefit from gaining familiarity with future nesting sites, and their participation in the antipredator defense of chicks is thought to be a group response, rather than alloparental care (Schmutz et al. 1982).

1.3.3.8. Summary of adoption and brood amalgamation in Anatidae

Adoption and brood amalgamation can be explained by mutual benefits for adopted young and foster parents in several goose species (tribe *Anserini*). In these species the dominance of a brood is positively related to its size. More dominant broods have access to a higher quality or quantity of resources, which may result in a higher growth rate of goslings. Growth rates in turn may be related to body size as an adult, and thus to several life history characters. The costs associated with larger broods may include more time spent with vigilance and less time for feeding for parents, increased investment in brood defense by parents, and increased intrabrood competition among chicks. These costs may limit the number of young a parent can rear in geese.

Several studies supported the ‘chick salvage strategy’ hypothesis in ducks (tribe *Anatini*). This hypothesis states that chicks deserted by their parents will seek adoption into alien broods to salvage their chances of survival. Adopting alien chicks appears not to influence the breeding success of adults; and thus, adoption may be neutral to the adopting parent. The dilution effect hypothesis was supported in Common Eiders, but some studies have reached somewhat different conclusions about the adaptive significance of brood amalgamation. For example, in this, and some other, duck species the physiological determination, ‘broodiness’ of the female also appears to be important in gathering large broods.

Many studies have reported no evidence of costs or benefits of adoption and brood amalgamation in waterfowl. Most of these studies found that the occurrence of amalgamation was related only to the density of broods at the feeding sites, and this led to the conclusion that adoption and brood amalgamation are accidental side effects of the high density of broods. In some species, brood amalgamation has been concluded to result from territorial aggression between females with the winner taking over the amalgamated brood. Kin selection and reciprocal altruism has been thought possible in Common Eiders by several studies, however, these hypotheses have not been tested.

1.3.4. Shorebirds (order *Ciconiiformes*, suborder *Charadrii* excluding family *Laridae*)

The parental care system of most shorebirds is similar to that of waterfowl in that the young feed themselves, and the broods leave the nest area soon after hatching. Similar to waterfowl, adoption and brood amalgamation may occur during brood movements or at the feeding sites (Jehl 1973; Hale 1980; Cooper & Miller 1992; Lanctot et al. 1995). However, shorebirds typically have smaller clutches than do ducks and geese, therefore, adoption may involve larger proportional changes in the fitness of adopting adults than is the case in waterfowl.

Adoption and brood amalgamation are thought to be frequent in shorebirds (Hale 1980; Pierotti 1988; Cooper & Miller 1992), and anecdotal evidence for adoption (e.g. Walters 1959; Bie & Ziljstra 1979; Flemming 1987) has been reported in numerous species (Skutch 1976; Johnsgard 1981; Cooper & Miller 1992). In spite of this, I do not know of any study that addresses the evolutionary significance of adoption and brood amalgamation in this large group of species. This may be because monitoring broods and quantifying fledging success in the field is often difficult for these species.

Brood amalgamation and adoption occur rarely, but regularly, in the Least Sandpiper (*Calidris minutilla*), mostly as a result of the high density of broods at feeding sites (Cooper & Miller 1992). Brood amalgamation has been thought to be important to chick survival, and to have a small impact on the fitness of adults. Benefits for either participant may include diluting the risk of predation or enhancing vigilance (Cooper & Miller 1992).

Forms of brood amalgamation in Bristle-thighed Curlews (*Numenius tahitiensis*) range from temporary associations of young broods through extended associations during the second week post-hatch to large associations (up to 10 broods) during the third and fourth week (Lanctot et al. 1995). Brood amalgamation appears to be important in this species because more than half of the broods participate in amalgamations and all broods that fledge young participate in amalgamations (Lanctot et al. 1995). Brood amalgamation is thought to enhance predator defense (by sharing vigilance and confusing predators), aid in the formation of pre-migrating juvenile flocks, and allow adults to migrate earlier (Lanctot et al. 1995). The physical dispersion of broods and increased detectability of larger broods may explain why brood amalgamations occurs only after the third week post-hatch (Lanctot et al. 1995).

The importance of brood size in the fledging success of shorebird chicks has been studied in Semipalmated Sandpipers (*Calidris pusilla*) (Safriel 1975). The survival of chicks was lower in experimentally enlarged broods than in control broods because enlarged broods consisting of five chicks were more likely to disappear than four-chick controls (Safriel 1975). Predators appear to detect larger broods more easily and tend to take the entire brood once a chick is detected (Safriel 1975). A predator-prey model indicates that if chicks use crypsis to avoid predation (as shorebirds) and detectability increases with brood size, then aggregation is beneficial for small or large groups, but not for groups of intermediate sizes (Taylor 1977). Most shorebirds have clutches of four eggs, and the addition of one or more young may still result in an intermediate-sized brood at which aggregating is not beneficial.

Brood size may also affect the time budget of parents. Time spent with parental behaviors appears to increase, and the time spent with feeding by parents appears to decrease, with increasing brood size in two of four species of lapwings (Walters 1982). In the other two species, the distance between the vigilant parent and the chicks increases with brood size (Walters 1982), which may lead to a higher vulnerability of chicks to predation. These findings support the hypothesis that brood size may be important in the trade-off between parental and self-maintenance behaviors (Walters 1982). Thus, the time required for parental behavior may limit the number of young for which the adults can care and still meet their energy requirements (Winkler & Walters 1983).

Even though the above studies have provided valuable insights into the occurrence, and the probable fitness costs and benefits of brood amalgamation and adoption in shorebirds, none of them tested hypotheses of the adaptive value of adoption and brood amalgamation. Therefore, further study is needed to understand the costs and benefits of adoption and brood amalgamation in this large group of species (Cooper & Miller 1992).

1.3.5. Gulls, terns, auks and murres (order *Ciconiiformes*, family *Laridae*)

1.3.5.1. Natural history of adoption

In this family, the chicks are able to leave the nest at a very early age, however, they usually stay in the vicinity of the natal nest where their parents feed them. Adoptions are usually initiated by chicks that wander from the natal territory (gulls and terns), or that solicit parental care from unrelated adults (auks and murres). Chicks wandering in the nesting colony can gain access into an alien brood either temporarily (in which case they usually are referred to as 'runners'), or permanently ('adoptees'). The annual proportion of adopting pairs in gulls and terns usually ranges from 5% to 35% (Brown 1998).

Adoption of alien chicks has been studied extensively in *Laridae*. This high interest may arise from the general view that these birds invest heavily into their young by feeding them, and therefore, adoption should be selectively costly for adults. However, adoption can be found in numerous gulls and terns. Before the late eighties, adoption was usually considered from the perspective of the parents, and the fitness of chicks has been in the focus only since a seminal paper by Pierotti & Murphy (1987). The new approach was based on the idea that offspring can be subject to natural selection (Trivers 1974).

1.3.5.2. Intergenerational conflict

Most studies of gulls and terns have supported one or several predictions of the intergenerational conflict hypothesis (Pierotti & Murphy 1987). This hypothesis states that adoption arises from a drive by chicks receiving inadequate parental care in their natal brood to seek adoption into broods in which they receive adequate parental care. The hypothesis has several predictions (Pierotti & Murphy 1987; Hébert 1988; Brown 1998). First, chicks receiving inadequate parental care should be more likely to leave their natal brood than chicks receiving standard parental care. Second, wandering chicks should establish themselves in broods in which they are larger, older, or more dominant than the resident chicks. Third, chicks seeking adoptions should show behavioral modifications that enhance the success of adoption. Finally, foster chicks should increase their fitness by adoption. In the next section, I review the evidence for each of these predictions.

1.3.5.3. Are departing chicks disadvantaged?

Inadequate parental care for chicks in their natal brood can result from several factors. First, in several gull and tern species hatching asynchrony results in age and body size differences among chicks within a brood (Morris 1988; Morris et al. 1991). The oldest and largest chicks are usually more dominant than younger and smaller chicks. This difference has been considered adaptive because it provides a potential for brood reduction for parents in years when environmental conditions limit reproduction (Mock 1984). Older chicks have been found to be more dominant over younger chicks and often evict them from the nest in the Black-legged Kittiwake (*Rissa tridactyla*) (Pierotti & Murphy 1987; Roberts & Hatch 1994). Asynchronous hatching also leads to a feeding hierarchy within the brood with the older chicks receiving proportionally more food than younger chicks. First-hatched or second-hatched chicks tend to be heavier at hatching and receive more food than do third-hatched chicks in the Common Tern (*Sterna hirundo*) (Langham 1972; Morris et al. 1991). Lower rates of parental provisioning lead to lower survival for later-hatched chicks in several species. Chick survival decreases with hatching order in the Common

Tern (Morris et al. 1991). Third-hatched chicks in Ring-billed Gulls (*Larus delawarensis*) have less than half the chance of fledging than first-hatched or second-hatched chicks (Brown 1998).

Second, individual variation in parental abilities may influence whether chicks receive adequate parental care or not. In the Ring-billed Gull, parents from which chicks depart feed their remaining young less frequently than parents whose chicks do not leave the natal brood (Brown et al. 1995). Similarly, more chicks depart from broods that are fed less frequently in Audouin's Gull (*Larus audouinii*) (Oro & Genovart 1999). In Black-legged Kittiwakes, first-hatched chicks may leave their natal nest and seek adoption elsewhere if parents neglect the nest (Roberts & Hatch 1994). Chicks that depart from their own brood tend to be fed poorly compared to resident chicks in the foster brood in the little tern (*Sterna albifrons*) and the common tern (Saino et al. 1994).

Finally, environmental conditions may limit the number of chicks that parents can provision, and chicks may be fed at lower rates than would be necessary for survival. For example, more chicks tend to be runners in years when food availability is low than in years when it is high in the Western Gull (*Larus occidentalis*) (Pierotti & Murphy 1987) and in Audouin's Gull (Oro & Genovart 1999).

Disadvantaged chicks, that receive sub-optimal parental care, have the option of seeking parental care elsewhere (Pierotti & Murphy 1987) and selection on chicks to depart when receiving inadequate care from parents must be strong (Morris et al. 1991). Several studies provide evidence that chicks leaving the natal brood hatch later, receive less food and grow slower than chicks remaining in their natal brood in the Herring Gull (*Larus argentatus*) (Graves & Whiten 1980; Pierotti & Murphy 1987; Pierotti 1988). In the Western Gull, departing chicks tend to be fed at lower rates than chicks staying in their own brood (Pierotti & Murphy 1987). In the Ring-billed Gull, departing chicks weigh less for their age than is predicted by a survival curve, and their growth curve was similar to that of chicks which eventually died (Brown 1998). Wandering chicks are typically the smallest, or the second smallest, chicks in their natal brood in Black Skimmers (*Rynchops niger*) (Quinn et al. 1994).

These findings suggest that chicks which leave their natal nest may do so because they receive inadequate parental care. This is further supported by the observation that in the Great Black-backed Gull (*Larus marinus*) in which runners and non-runners did not differ in growth rate, feeding rate, or body mass, the wandering of chicks did not lead to permanent adoptions, only to temporal alloparental care (Pierotti & Murphy 1987).

1.3.5.4. Wandering chicks and target broods

Most studies of *Laridae* suggest that only a small proportion of departing chicks gain permanent adoption into alien broods, and chicks can establish themselves in broods if they are not smaller than the youngest resident chick. In the Black-legged Kittiwake, chicks generally make more than four movements in and out of nests before settling in one and only 7 of 12 wandering chicks were adopted (Roberts & Hatch 1994). In the Herring Gull, the proportion of adopted chicks was 53% (n = 19) in one study (Graves & Whiten 1980) and 19% (n = 280) in another (Pierotti & Murphy 1987). In the Common Gull (*Larus canus*), 23% of wandering chicks (n = 81) were adopted whereas at least 14% were rejected or even killed by the alloparents (Bukacinski et al. 2000). Successful chicks in this species were the same age as, or older than, chicks in target broods (Bukacinski et al. 2000). In the Ring-billed Gull, 34 of 47 departing chicks gained adoptions and the rest were runners (Brown et al. 1995). Adoptees usually were older than the oldest resident chick in the foster brood, whereas runners usually were younger than resident chicks (Brown et al. 1995). In another study of the same species, 76% of the adopted chicks were older than the oldest resident chick, and adopted chicks did not fledge if they were younger than resident chicks (Brown 1998). In the Western Gull, 23% of the chicks (n = 707) departed their natal brood, and 21% of them gained adoptions (Pierotti & Murphy 1987). Chicks gaining permanent adoption into a foreign brood tend to be the smallest and slowest growing chicks in their natal brood, and they are usually as large as the largest resident chick in the foster brood (Pierotti & Murphy 1987). In the Common Tern, foster chicks similar in age to the youngest resident chick usually are runners, whereas chicks that are older than the youngest resident chick usually gain permanent adoption, and are likely to fledge (Morris et al. 1991).

These observations indicate that wandering chicks gain adoptions into broods in which the chances of dominating the younger resident chicks are high. Holley (1988) presented an alternative explanation on why chicks gain adoptions in younger broods. He suggested that this could be caused by the behavior of the resident chicks, which can attack the foster chick and may thus influence the success of adoption. If the foster chick is younger than the resident chicks, it may be expelled from the nest by the resident chicks (Holley 1988). The scant evidence for this hypothesis (Pierotti et al. 1988) offers little support for this idea because resident chicks are rarely aggressive towards alien chicks. However, more recent evidence (Roberts & Hatch 1994) shows that Black-legged Kittiwake chicks entering alien broods are often attacked by the resident chicks. Aggression from resident chicks, and not from adults, was the main problem for chicks seeking adoption in this species (Roberts & Hatch 1994). In other species, however, aggression among chicks may decrease after adoption. The level of aggression among chicks is lower in adopting broods than in non-adopting ones in Audouin’s Gull (Oro & Genovart 1999).

The spatial pattern of nests also may be important in determining the success of wandering chicks. Adoptions are more frequent than rejections among neighbors in the Common Gull (Bukacinski et al. 2000). The natal nests of adopted chicks were significantly closer to the nests of foster adults than the natal nests of chicks that got rejected (Bukacinski et al. 2000).

1.3.5.5. Chick behavior facilitating adoption

Chicks can manipulate parents into adopting them either by their position in the nest or by their behavior. First, if chicks are in, or close to, the nest, parents tend to be reluctant to attack them. In Herring Gulls, alien chicks gaining access into a brood spend more time on, or close to, the nest than do resident chicks, tend to escape to the nest when chased and crouch with the resident chicks (Graves & Whiten 1980). These foster chicks exploit an apparent inhibition of the adults to attack chicks in the nest (Graves & Whiten 1980). The position of the chicks is also important in Common Terns because parents are behaviorally inhibited against attacking young in, or near, the nest cup (Morris 1988). Similarly, Black-legged Kittiwake adults accept young in the nest and attack young outside the nest, suggesting that the position of the chick is of primary importance in recognition (Roberts & Hatch 1994).

Second, when foster chicks behave ‘positively’ towards the parent, it may be more difficult for the parents to recognize them. In Herring Gulls, choice tests suggested that the parent-young recognition is based on the behavior of the young and it can be exploited by any chick seeking adoption (Knudsen & Evans 1986). When chicks are exchanged among broods in the Ring-billed Gull, the parents accept those chicks that approach them, are not sedentary and do not retreat even after being pecked at by parents (Brown 1998). Chicks deprived of food approached foster parents as frequently as did resident chicks (Brown 1998). These observations support the prediction that chicks may use behavioral actions to manipulate adults into adopting them.

1.3.5.6. Benefits of foster chicks

Chicks may benefit from adoption by receiving more food, and thereby having a higher growth rate and fledging success. Adopted Western Gull chicks were fed at higher rates in the foster brood than they were in their natal brood (Pierotti & Murphy 1987). In Herring Gulls, growth rate of foster chicks increased significantly after adoption (Pierotti & Murphy 1987). The growth rate of chicks largely determines their fledging success. For example, Ring-billed Gull chicks that leave their natal broods double their chances of survival from 22% in the natal brood to 44% in the foster brood (Brown 1998). Adopted chicks usually survive to fledging if they are older than the oldest resident chick (Brown et al. 1995). Similarly, in Audouin's Gull, foster chicks survive to fledging only if they are older than the oldest resident chick (Oro & Genovart 1999). In the Black-tailed Gull (*Larus crassirostris*), the fledging success of experimentally exchanged chicks is highest when the age difference between the adopted and resident chicks is small (< 2 days), whereas it decreased with increasing age difference (Narita 1994). Adoptees in Little and Common Terns have the same chances of survival as the resident chicks (Saino et al. 1994). In the Black Skimmer, the few chicks that have gained adoption survive longer than some or all of their resident foster siblings (Quinn et al. 1994).

The benefits for the foster chicks are unclear in the Black-legged Kittiwake, because chicks are expelled from the nest by their older siblings and do not 'choose' to leave (Roberts & Hatch 1994). However, chicks may be selected to seek adoption after being expelled from nests, if adoption increases their chances of survival.

1.3.5.7. Costs to adopted chicks

Chicks that leave their natal broods experience risks because adults may attack, and even kill, wandering chicks in several species. In Herring Gulls, chicks seeking adoption are often attacked and killed by adults (Graves & Whiten 1980). Pierotti & Murphy (1987) found that 27% of runners are killed Herring Gulls and 35% of the departing chicks died in Western Gulls. When chicks of Ring-billed Gulls are exchanged among broods, 9% of the rejected chicks were killed by the adults (Brown 1998). In Little Terns, wandering chicks experienced higher mortality than did resident chicks, indicating risks of leaving the natal brood (Saino et al. 1994).

Infanticide in gulls has been hypothesized as a parental strategy to avoid adoption (Mock 1984; Pierotti & Murphy 1987; Pierotti 1991). An alternative explanation for infanticide is territorial defense by adults against conspecific young. Territorial aggression is supposed to account for killing of chicks in the Western Gull (Hunt & Hunt 1975). In the Black Skimmer and the Common Tern, infanticide has been thought to be best explained by the intergenerational conflict hypothesis and not a side-effect of territoriality (Quinn et al. 1994). However, this idea has not been tested rigorously.

1.3.5.8. Costs to foster parents

The costs of adoption to adults may include lower rates of food provisioning for the chicks, and lower growth rate and fledging success of resident chicks. Adoption has led to a reduction in food intake by resident chicks in Herring Gulls (Graves & Whiten 1980). There is a negative correlation between the proportion of food brought to foster chicks and seasonal survival of resident chicks, indicating costs for resident chicks and foster parents in Little and Common Terns (Saino et al. 1994). Adopting parents fledge fewer of their own young than do non-adopting parents in Common Terns (Morris et al. 1991). The breeding success of adopting adults is lower than that of non-adopting adults in Audouin’s Gull (Oro & Genovart 1999). Adopting pairs fledge fewer young than do control pairs or pairs that had a chick depart their brood in the Ring-billed Gull (Brown et al. 1995). The annual cost of adoption was -0.5 fledged young per pair, whereas the benefit to donor pairs was 0.3 chicks per year in this species (Brown 1998). These estimates suggest that donors may parasitize adopting adults. However, this is unlikely to be of primary importance in adoption because the disadvantaged status of chicks seeking adoption appears to be more important in why adoptions occur and because chicks face a considerable risk of being rejected or killed.

The costs of adoption vary according to when adoption takes place during brood-rearing. In Western Gulls, adoption reduces the survival of the resident chicks only when adoption occurs early and small and young chicks are adopted (Carter & Spear 1986). Late adopters incur smaller costs than do early adopters or they may even benefit from adoption (Carter & Spear 1986). Similarly, adoption of larger chicks does not incur costs for parents in Herring Gulls (Holley 1981). However, if adults adopt chicks while they still incubate eggs, they may abandon incubation and lose their eggs. The hatching success of adopting parents decreased in Herring Gulls (Graves & Whiten 1980). In Black-legged Kittiwakes, the wandering chicks typically are adopted by adults incubating eggs, and foster parents abandon incubation and care for the adopted chick (Pierotti & Murphy 1987; Roberts & Hatch 1994). Adoption leads to the complete loss of the eggs, therefore, adoption involves high costs for foster parents in Black-legged Kittiwakes (Pierotti & Murphy 1987; Roberts & Hatch 1994).

Adoption is not necessarily costly in all gull species. For example, the fledging success of resident chicks was not reduced in five cases of adoption in the Western Gull (Hunt & Hunt 1975). In the Herring Gull, there is experimental evidence that parents can adjust their investment into feeding larger broods (Haymes & Morris 1977). The growth rate and fledging success of adopted and resident chicks was similar in enlarged, control and reduced broods (Haymes & Morris 1977).

If adoption is costly for parents, why has this behavior not been eliminated by selection? Several hypotheses have been proposed to explain this. First, the adopter and adoptee can be related, and the costs incurred by lower fledging success of genetic young may be outweighed by the benefits obtained by rearing a related chick. This hypothesis has been thought to be unlikely in gulls and terns because of the low philopatry of both adults and young, the lack of kin nesting groups and because adults kill young or may adopt chicks of other species (Pierotti & Murphy 1987). New evidence, however, suggests that kin selection may work in some species (see below).

Second, the reciprocal altruism, and the intergenerational conflict, hypotheses are not mutually exclusive (Pierotti & Murphy 1987). In other words, even though adoption is costly, the benefits for the donor may exceed the costs for the recipient, and if adults return the favor by changing roles between breeding attempts, the altruistic act of adoption may be adaptive (Trivers 1971). This hypothesis has been thought plausible in several species of gulls and terns (Pierotti 1980, 1982), however, it has been tested only in the Ring-billed Gull. The costs to the foster parent of rearing an alien chick (-0.5 fledged chick per pair) outweighs the benefits of adoption to the donor (0.3 fledged chick per pair) in this species, and there was no sign of reciprocating between adults (Brown 1998). However, in Audouin's Gull parents whose chick departs have higher breeding success than do adopting pairs (Oro & Genovart 1999). This 'interpair conflict' (Oro & Genovart 1999) makes reciprocal altruism possible, however, the existence of reciprocating between parents remains unclear.

Third, the true 'soft altruism' hypothesis states that there may be selection for adoption if it involves only low costs (Pierotti & Murphy 1987). The selection pressure on offspring may be so great that adults have no alternative but to act as true 'soft altruists' (Wilson 1980; Pierotti & Murphy 1987). The costs of adoption may be relatively lower in birds nesting under extreme environmental conditions, and in which most chick mortality is density-independent (Pierotti & Murphy 1987).

Finally, a recognition error by parents may lead to adoption (Tinbergen 1953). The parent-young recognition system should minimize errors, therefore, it should decrease the probability of incorrectly identifying genetic offspring as non-filial (Knudsen & Evans 1986). This is because a recognition error, i.e., mistaking a resident chick for an alien and attacking or even killing it should be highly costly (Knudsen & Evans 1986). This potential risk may explain why early chick recognition by parents is not well developed in adults (Pierotti & Murphy 1987). For example, in the Black-tailed Gull 81% of the experimentally exchanged chicks (n = 74) were accepted and adopted by foster parents with young chicks (< 6 days), regardless of the age difference between foster chicks and resident chicks (Narita 1994).

Adults do recognize chicks later to avoid adoption, which is indicated by the fact that at least 27% of runners are killed by adult Herring and Western Gulls (Pierotti & Murphy 1987). Adults usually recognize their young just before the chicks are able to leave the nest (Miller & Emlen 1975). In Audouin's Gulls, recognition occurs after seven days of age, and no adoptions have been observed after this age (Oro & Genovart 1999). Pairs with young chicks are more likely to accept alien young than are pairs with older chicks in Ring-billed Gulls (Brown et al. 1995; Brown 1998). Adoptions occur infrequently and usually before chick recognition develops in parents, which supports the recognition error hypothesis (Brown 1998). The calculated costs and benefits of adoption indicates that the life-time cost to an adult adopting one chick is a 4% decrease in fitness, whereas the cost of incorrectly identifying and chasing away its own chick is an 8% decrease in fitness (Brown 1998).

Inefficient chick recognition is clearly maladaptive at current nesting densities in Herring Gulls (Holley 1984). The ability to recognize one's own chick in this species has been thought to differ among nesting sites (Holley 1984) because cliff-nesters accept older chicks, whereas pairs nesting in flat areas, where the chance of encountering wandering chicks is high, accept only young chicks (von Rautenfeld 1978).

Recognition of chicks by parents may be unnecessary, if the chances of encountering chicks seeking adoptions are small. In such cases there may be high costs associated with evolving chick discrimination mechanisms (Pierotti & Murphy 1987; Pierotti 1991). In long-lived birds, the chances of adoption are usually small. In Western Gulls, adults have an 8-10% chance annually of rearing alien young and a 50% chance of doing so during their entire life (Pierotti & Murphy 1987). Herring Gulls face a 5-6% annual chance of rearing alien young (Pierotti & Murphy 1987). Thus, the chance of rearing alien young may be low, and evolving chick recognition under such conditions can be costly (Brown 1998).

1.3.5.9. Alternative hypotheses of adoption in Laridae

Adoption might be maladaptive in Herring Gulls nesting in high densities (Holley 1981). Dense colonies may result from a decline in the availability of nesting habitats where the nests can be spaced out. Adoption may have never occurred in colonies with greater nest dispersion, and may be a recent phenomenon occurring under extreme conditions. Therefore, it is possible that there has not been enough time for selection to act on the behavior in Herring Gulls (Holley 1981). Similarly, the newly occupied habitat also may influence the occurrence of adoptions in Audouin’s Gulls (Oro & Genovart 1999). High nesting densities also have been thought important in the occurrence of adoption in Western Gulls (Carter & Spear 1986) and Little and Common Terns (Saino et al. 1994). In spite of these suggestions, high density alone is unlikely to explain the widespread occurrence of adoption in gulls, because it is unlikely that recent changes affected all species the same way.

In murres, chicks may solicit parental care from unrelated adults, sometimes even when the genetic parents are present (Birkhead & Nettleship 1984; Gaston et al. 1995). These attempts typically lead to some form of alloparental care (e.g. brooding, feeding), but sometimes they result in complete adoptions, for example, in the Thick-billed Murre (*Uria lomvia*) (Gaston et al. 1995). Alloparenting has been considered non-adaptive for adults (usually failed breeders), but beneficial for chicks in the Common Murre (*Uria aalge*) (Birkhead & Nettleship 1984). Chicks were thought to manipulate and exploit the brooding tendencies of failed breeders, which were still stimulated to provide parental care by high hormone levels (Birkhead & Nettleship 1984).

The parenting experience hypothesis of adoption has been thought unlikely in gulls and terns because adopting adults usually have chicks on their own at the time of adoption (Hunt & Hunt 1975; Pierotti & Murphy 1987). In the Ring-billed Gull, the donor and foster parents were neither inexperienced (85% had chicks before), nor failed breeders (Brown 1998).

1.3.5.10. Sociobiological hypotheses in Laridae

Kin selection may explain adoption (Waltz 1981; Pierotti 1982), however, the methods to test this hypothesis rigorously have only recently become widely available. In the context of alloparental care, molecular methods have been applied to identify adoption. For example, Millar et al. (1997) used minisatellite DNA fingerprinting to detect adoption in the south polar skua (*Catharacta maccormicki*).

Kin selection has long been thought possible in murres because kin may nest close to each other and adoptions usually occur among neighbors (Birkhead & Nettleship 1984; Gaston et al. 1995). This hypothesis is supported by allozyme and DNA-fingerprinting studies of Thick-billed Murres (*Uria lomvia*) in which individuals nesting in the same subcolony comprise extended family groups (Friesen et al. 1996). In this species, the average level of relatedness of individuals was 0.10, and Hamilton’s (1971) equation suggests that adoption could be adaptive if the net fitness benefits exceed 10 times the net fitness costs of the foster parent (Friesen et al. 1996). However, this study did not explicitly investigate the role of kin selection in actual adoption events.

Brown (1998) used DNA fingerprinting to test predictions of the kin selection hypothesis in Ring-billed Gulls, in which adoptions occur among neighbors. Based on estimates of genetic relatedness, the neighbors are not more closely related than are spatially segregated individuals, thus, the kin selection hypothesis was not supported in this species (Brown 1998). In contrast, the kin selection hypothesis is supported in Common Gulls (Bukacinski et al. 2000). Genetic similarity has been found to be higher between adopted chicks and foster parents than between adopted chicks and randomly selected males or between rejected chicks and rejecting parents (Bukacinski et al. 2000). Adopted chicks show genetic relatedness to neighboring foster parents but not to non-neighboring pairs (Bukacinski et al. 2000). The degree of relatedness between adopters and adoptees usually is high enough to compensate for the lower survival of the parents' own chicks (Bukacinski et al. 2000).

Some authors suggest that chicks can also behave altruistically due to to kin selection. Departing chicks may enhance their inclusive fitness by leaving the brood, which allows the parents to invest more heavily in the parental care of their siblings, and thus increasing their siblings' chances of survival (Saino et al. 1994). I am unaware of any studies that have explicitly investigated this hypothesis.

Group selection has also been invoked to explain adoption in gulls and terns (Pierotti & Murphy 1987). This hypothesis suggests that adoption increases the fitness of the group in which it occurs. Although this hypothesis may provide a partial explanation of the adaptive value of adoption (Pierotti & Murphy 1987), its strict assumptions of closed and isolated nesting groups make it unlikely in *Laridae*. Immigration rates in most species are too high to be compatible with the maintenance of an altruistic behavior (Holley 1981).

1.3.5.11. Summary of adoption in Laridae

Most studies in the semi-precocial *Laridae* support at least one prediction of the intergenerational hypothesis. The fact that chicks are fed by parents emphasizes the importance of parental care, and the fitness costs and benefits associated with it are more likely to determine the reproductive decisions of adults and young in species in this family than in precocial birds. Chicks may be selected to solicit parental care from adults in case they receive inadequate care in their natal brood. Adults may be selected to recognize their chicks in order to restrict parental care to their own offspring. These selective forces of opposite directions create the intergenerational conflict (Pierotti & Murphy 1987). The best evidence for the intergenerational conflict is provided by the non-random pattern in departures of chicks from natal broods (Pierotti & Murphy 1987; Brown 1998). Leaving the natal brood in case their survival chances are low may be adaptive for chicks, and there is a substantial body of evidence that disadvantaged chicks are those that depart from their natal broods. Foster parents usually incur costs by adoption, therefore, there should be selection against this behavior. However, the recognition system of parents may develop after chicks become mobile because of physiological or evolutionary constraints. The frequency of adoption observed in various species may represent a trade-off between the costs of adoption and avoiding it (Sherman et al. 1997). Therefore, it may be more appropriate to focus on selection acting on the recognition system itself rather than on adoption (Brown 1998).

There is a large asymmetry in benefits to chick and costs to the foster parent, which arises from two factors. First, chicks risk death by leaving the natal brood, whereas by adopting alien chicks adults risk some reproductive effort only (Pierotti 1988). Second, selection can act more strongly on the trait that is expressed in an earlier life stage than on one expressed in a later stage (Charlesworth 1980; Pierotti 1991; Brown 1998). This asymmetry in the fitness costs and benefits can influence the outcome of the intergenerational conflict (Pierotti 1988), and disadvantaged chicks that gain adoption into foreign broods should ‘win’ the intergenerational conflict at the expense of the foster parents (Morris et al. 1991; Brown 1998).

1.3.6. Cormorants (order *Ciconiiformes*, suborder *Ciconii*, family *Phalacrocoracidae*)

Cormorant chicks are altricial, and become mobile later during their development than chicks of precocial birds. However, the age of chick mobility precedes fledging, and young that are unattended by their parents form pre-fledging creches in several species of this clade. In Brandt’s Cormorant (*Phalacrocorax penicillatus*) creches occurred mostly at night and at cooler air temperatures, which suggests that creches may be important in the thermoregulation of the chicks (Carter & Hobson 1988). An alternative advantage of creches is that it may facilitate the development of fledgling behaviors (Carter & Hobson 1988).

1.3.7. Flamingos (order *Ciconiiformes*, suborder *Ciconii*, family *Phoenicopteridae*)

Flamingo chicks form creches after the age of 10 days, and parents are believed to be able to find their chicks in large groups of chicks (Kear 1970). The creching behavior of flamingo chicks and the alloparental behavior of adults are similar to those of penguins (Jouventin et al. 1995).

The function of creches in flamingos is unclear. Some authors believe that creches provide protection against predators because the chicks tend to crowd together if they are approached by intruders and the creche becomes more packed if alarm calls are given by attending parents (see Kear 1970 and references therein). Mobile young aggregate in creches after disturbance by humans in the Greater Flamingo (*Phoenicopterus roseus ruber*) (Brown et al. 1973). Creching by flamingo chicks, therefore, may be advantageous because individual chicks may decrease the chances of their being predated in creches. However, the lack of tests of this and other hypotheses precludes drawing conclusions at this time.

1.3.8. Pelicans (order *Ciconiiformes*, family *Pelecanidae*)

In pelicans chicks become mobile later than chicks of precocial species, but they do so before they are able to fly. Creching occurs when chicks aggregate in groups while the adults are away from the colony. Adults are able to find their own chick in the creche, and restrict parental care only to them (Schaller 1964). The main hypotheses for creching are protection from predators or from adult aggression, thermoregulation, and inadvertent result of crowding.

In the Great White Pelican (*Pelecanus onocrotalus roseus*), chicks may form creches of up to 100 young or more and creche formation may be advantageous for thermoregulation during cold nights (Brown & Urban 1969). In the White Pelican (*Pelecanus erythrorhynchos*), creches of unattended chicks form through the social attraction among chicks, facilitated by disturbance from predators and humans (Evans 1984). Creches tend to be largest at night and dispersed throughout the day (Schaller 1964). The density within a creche is negatively related to air temperature (Schaller 1964; Evans 1984). Laboratory measurements indicate that the energy saving due to creching is small but significant (Evans 1984). These studies suggest that creches protect chicks from temperature extremes, but predation also may be a proximate factor in the formation of creches.

1.3.9. Penguins (order *Ciconiiformes,* family *Spheniscidae*)

Penguin chicks typically form creches when left unattended by parents (Evans 1980; Davis 1982). Creches have been proposed to provide protection for the chicks against either predators (Stonehouse 1960; Davis 1982), harsh weather (Davis 1982), or attacks by conspecific adults (Seddon & van Heezik 1993). Parents usually find their chicks in the creche, however, alloparental care also has been reported in some species (Stonehouse 1960; Jouventin et al. 1995; Wienecke 1995).

In the Emperor Penguin (*Aptenodytes forsteri*) and the King Penguin (*A. patagonica*) alloparents tend to be non-breeding birds or birds whose breeding failed (Stonehouse 1960, Jouventin et al. 1995). Females of these species return to the colony for the first time after egg-laying several weeks after their chick hatches. If the returning females have lost their egg or chick during the time they spent away from the colony, it is likely that social stimulation and their endocrinological determination (high prolactin levels) predispose them to accept alien chicks or even kidnap chicks from other adults (Jouventin et al. 1995). Because chick-rearing may comprise up to 32% of the total annual energy budget, adoption appears to be costly for alloparents. Adoptions, however, usually are temporary, and rarely last more than 10 days (Jouventin et al. 1995). The chicks solicit food and brooding from adults when they are left unattended by their parents. These observations support the intergenerational conflict hypothesis (Pierotti & Murphy 1987). Chicks can manipulate unrelated and hormonally predisposed adults into providing parental care and the endocrinological determination of females probably outweighs the costs of adoption. However, kin selection is also possible in Emperor Penguin colonies, which are highly isolated from each other (Jouventin et al. 1995). Finally, even though most alloparents were experienced breeders, adopting sub-adults may gain breeding experience (Jouventin et al. 1995).

The intergenerational conflict hypothesis has been also supported by studies in other penguin species. In Little Penguins (*Eudyptula minor*) chicks that are abandoned by their parents wander in the colony and sometimes become adopted into broods of similar age (Wienecke 1995). These chicks benefit from adoption by increasing their chances of survival, whereas adoption is costly for adults because they risk losing their genetic offspring (Wienecke 1995).

1.4. CONCLUDING REMARKS

Recent years have brought considerable progress in understanding adoption and brood amalgamation in precocial birds. Traditionally, adoption and brood amalgamation were approached from the perspectives of altruism and cooperation among adults. Many recent studies, however, suggest that adoption and brood amalgamation can be associated with fitness benefits for either the adopter or the adoptee, especially in clades in which parental care is shareable (non-depreciable, Lazarus & Inglis 1986). These studies show numerous ways in which adoption and brood amalgamation can be favored by selection and suggest that the fitness costs and benefits of alloparental care can be more complex than previously thought.

This review summarizes recent hypotheses and findings. It also presents a framework of testable proximate hypotheses based on fitness costs and benefits for both the alloparent and the foster chick. Previous frameworks of hypotheses (e.g. Pierotti & Murphy 1987; Eadie et al. 1988) have led to a surge of interest in adoption and alloparental care. However, the new studies have also advanced new hypotheses and have presented new data to evaluate the numerous competing hypotheses, and the surge of interest in alloparental care also introduced a confusion in terminology (e.g. Table 1.) and logic. For example, mechanistic hypotheses found in the literature usually are not mutually exclusive, and this review presents a remedy to part of this problem by making the distinction between fitness costs and benefits more explicit. Because more than one mechanism can be responsible for the patterns of adoption and brood amalgamation in some species, it is essential to address several hypothesized mechanisms simultaneously in order to test the adaptive significance of adoption and brood amalgamation. Researchers should attempt to test *a priori* predictions of the competing hypotheses (Eadie et al. 1988) by careful measurement of the costs and benefits that are possible based on the natural history of each species. To test hypotheses of non-adaptive mechanisms, one should make sure that all possible measures of fitness are considered (Emlen et al. 1991). Because the differences between explanations are often finite and costs and benefits may vary within as well as among species (Brown 1998), the study of different populations of the same species becomes a necessary element of a statistically valid approach to revealing evolution of adoption and brood amalgamation.

The review of the various taxa provides two important insights. First, our knowledge about the significance of adoption and brood amalgamation is solidly grounded in some clades of precocial birds, for example, in *Anatidae* (ducks and geese) and in *Laridae* (gulls, terns and alcids). Most studies of geese show mutual benefits for alloparents and foster young, and the benefits are mostly associated with the advantages of larger brood sizes in geese. In most ducks alloparental care provides benefits for chicks that are deserted by their parents and it is neutral or slightly beneficial for alloparents. In gulls and terns, adoption usually provides benefits for chicks whereas alloparents generally incur costs by adoption. Behavioral and developmental constraints prevent the parents from avoiding these costs and disadvantaged chicks can win the intergenerational conflict possibly because of the large asymmetry between the costs of adoption to the parent and the benefits of being adopted to the young.

Additionally, our understanding of the adoption behavior of some clades of birds is far from complete. There are numerous anecdotal reports of adoption and brood amalgamation in galliform birds and shorebirds, however, the evolutionary significance of these behaviors has not been addressed in these speciose clades. The increasing availability of powerful methods (field methods: radio telemetry, modeling: evolutionarily stable strategies, game theory, molecular methods: DNA-fingerprinting, population structure studies using genetic markers) makes the testing of hypotheses in these diffcult taxa more feasible.

In conclusion, the study of adoption and brood amalgamation provides a new insight into the reproductive strategies of precocial birds and the fitness costs and benefits associated with these strategies. These studies illuminate the evolution of alloparental care and challenge previous views of altruism and cooperation (Eadie & Lyon 1998) by demonstrating relative benefits of adoption and brood amalgamation. The progress on adoption and brood amalgamation contributes to a better understanding of highly complex behavioral and social systems of animals.

1.5. TABLES

Table 1. A summary of the terminology used by previous studies for situations in which young from several broods merge in one functional unit and are reared by one or more adults or mated pairs.

Term used	**Taxon**	**References**
Brood amalgamation	Waterfowl	Savard 1987; Eadie et al. 1988; Afton 1993; Beauchamp 1997, 1998; Mitchell & Rotella 1997; Eadie & Lyon 1998; Savard et al. 1998; Öst 1999
	Shorebirds	Cooper & Miller 1992, Lanctot et al. 1995
Brood mixing	Waterfowl	Seddon & Nudds 1994; Nastase & Sherry 1997
Creching	Waterfowl	Bergman 1956; Koskimies 1955; Hori 1964, 1969; Gorman & Milne 1972; Williams 1974; Munro & Bedard 1977a, 1977b; Kehoe 1989; Bustnes & Erikstad 1991
	Cormorants	Carter & Hobson 1988
	Flamingos	Brown et al. 1973
	Pelicans	Schaller 1964; Brown & Urban 1969; Brown et al. 1973; Evans 1984
	Penguins	Stonehouse 1960; Davis 1982; Seddon & van Heezik 1993; Jouventin et al. 1995
Gang brooding	Waterfowl	Warhurst & Bookhout 1983
Pods	Pelicans	Schaller 1964; Brown & Urban 1969

Table 2. Precocial and some altricial bird species in which the evolution of adoption or brood amalgamation has been addressed qualitatively or tested quantitatively.

Species	References
Struthioniformes	
Greater Rhea (*Rhea americana*)	Codenotti & Alvarez 1998; Lábaque et al. 1999
Galliformes	
Ruffed Grouse (*Bonasa umbellus*)	Maxson 1978
Merriam's Wild Turkey (*Meleagris gallopavo*)	Mills & Rumble 1991
Anseriformes	
Pink-footed Goose (*Anser brachyrhynchus*)	Lazarus & Inglis 1978
Bar-headed Goose (*A. indicus*)	Schindler & Lamprecht 1987
Lesser Snow Goose (*Chen c. caerulescens*)	Williams 1994
Canada Goose (*Branta canadensis*)	Warhurst & Bookhout 1983; Seddon & Nudds 1994; Nastase & Sherry 1997; Gosser & Conover 2000
Barnacle Goose (*B. leucopsis*)	Black & Owen 1989a; Choudhury et al. 1993; Forslund 1993; Larsson et al. 1995; Loonen et al. 1999
Trumpeter Swan (*Cygnus cygnus buccinator*)	Mitchell & Rotella 1997
Shelduck (*Tadorna tadorna*)	Hori 1964, 1969; Williams 1974; Patterson et al. 1982
Mallard (*Anas platyrhynchos*)	Titman & Lowther 1975
Lesser Scaup (*Aythya affinis*)	Afton 1993
Blue-winged Teal (*Anas discors*)	Rohwer 1985
Common Eider (*Somateria mollissima*)	Ahlén & Andersson 1970; Gorman & Milne 1972; Munro & Bedard 1977a, 1977b; Schmutz et al. 1982; Bustnes & Erikstad 1991; Erikstad et al. 1993; Öst 1999; Öst & Kilpi 2000
Surf Scoter (*Melanitta perspicillata*)	Savard et al. 1998
White-winged Scoter (*Melanitta fusca*)	Koskimies 1955; Kehoe 1989
Bufflehead (*Bucephala albeola*)	Savard 1987
Goldeneye (*Bucephala clangula*)	Andersson & Eriksson 1982
Barrow's Goldeneye (*Bucephala islandica*)	Savard 1987; Eadie & Lyon 1998
Goosander (*Mergus merganser*)	Bergman 1956
Red-breasted Merganser (*M. serrator*)	Bergman 1956
Ciconiiformes	
Least Sandpiper (*Calidris minutilla*)	Cooper & Miller 1992
Bristle-thighed Curlew (*Numenius tahitiensis*)	Lanctot et al. 1995
Piping Plover (*Charadrius melodus*)	Flemming 1987
Common Gull (*Larus canus*)	Bukacinski et al. 2000
Ring-billed Gull (*L. delawarensis*)	Miller & Emlen 1975; Brown et al. 1995; Brown 1998
Herring Gull (*L. argentatus*)	Graves & Whiten 1980; Holley 1981, 1984; Knudsen & Evans 1986; Pierotti & Murphy 1987; Pierotti 1988
Western Gull (*L. occidentalis*)	Hunt & Hunt 1975; Carter & Spear 1986; Pierotti & Murphy 1987
Great Black-backed Gull (*L. marinus*)	Pierotti & Murphy 1987
Audouin's Gull (*L. audouinii*)	Oro & Genovart 1999
Black-legged Kittiwake (*Rissa tridactyla*)	Pierotti & Murphy 1987; Roberts & Hatch 1994
Common Tern (*Sterna hirundo*)	Morris 1988; Morris et al. 1991; Quinn etal. 1994; Saino etal. 1994
Little Tern (*S. albifrons*)	Saino et al. 1994
Black Skimmer (*Rynchops niger*)	Quinn et al. 1994
Common Murre (*Uria aalge*)	Birkhead & Nettleship 1984
Thick-billed Murre (*Uria lomvia*)	Gaston et al. 1995; Friesen et al. 1996
Brandt's Cormorant (*Phalacrocorax penicillatus*)	Carter & Hobson 1988
Greater Flamingo (*Phoenicopterus roseus ruber*)	Brown et al. 1973
Great White Pelican (*Pelecanus onocrotalus roseus*)	Brown & Urban 1969; Brown et al. 1973
White Pelican (*P. erythrorhynchos*)	Schaller 1964; Evans 1984
Emperor Penguin (*Aptenodytes forsteri*)	Jouventin et al. 1995
King Penguin (*A. patagonica*)	Stonehouse 1960
Little Penguin (*Eudyptula minor*)	Wienecke 1995

Table 3. A matrix of proximate cost-benefit hypotheses of adoption and brood amalgamation in birds with precocial young. Adaptive hypotheses make up the first row and first column of the table; non-adaptive explanations are underlined.

		ADOPTING ADULT		
		Benefit	**Neutral**	**Cost**
ADOPTED CHICK	**Benefit**	Detection of predators Defense against predators Dilution effect Enhanced dominance of larger broods Heat conservation	Access to non-limiting resources Chick salvage strategy Mutual attraction of chicks	Intergenerational conflict Heat gain during brooding
	Neutral	Adult parenting experience Diluting effect Signal for adult quality Mutual attraction of adults	Neutralism (accidental mixing) Side-effect of territoriality	Adult error
	Cost	Exploitation of foster young through a selfish herd effect Exploitation of foster young during brooding	Chick error	Maladaptation

CHAPTER 2. COLONIAL NESTING AND THE FACTORS INFLUENCING BREEDING SUCCESS IN AVOCETS

2.1. INTRODUCTION

Understanding the population dynamics of a species requires an understanding of the basic reproductive parameters (breeding success) and of the spatial organization of the populations. Shorebirds (suborder *Charadrii*) are especially suitable to study the link between breeding success and population size because both breeding success and population sizes show large annual variation, and the survival of adults and young, as well as the spatial organization (migration and connectedness) of populations, are well known in several species. Breeding success in shorebirds is thought to be influenced mainly by predation on eggs and young, and adverse weather, which mostly affects the survival of chicks.

Several studies have been conducted to explore the factors influencing breeding success in coastal populations of Avocets (*Recurvirostra avosetta*) in England, France, the Netherlands, Belgium and Germany (Cadbury & Olney 1978; Watier & Fournier 1980; Bie & Zijlstra 1985; Bouche 1991; Van Impe 1991; Hötker & Segebade 2000), and long-term monitoring of Avocet populations resulted in several long-term datasets on population sizes (Hagemeijer & Blair 1997). These studies provide support for both predation and weather being the main factors influencing breeding success in this species.

In spite of a wealth of information on coastal avocets, there are no data available on the breeding biology of the isolated inland populations of avocets in Europe. In this paper, I present data on the breeding biology of the largest of such inland populations, the Hungarian population. These data were collected to provide detailed information on breeding biology, with the additional objective of contributing a basis to an understanding of parental care and the social system of this species.

2.2. METHODS

2.2.1. Field methods

2.2.1.1. Study sites and study period

Fieldwork was carried out on alkaline lakes of the Kiskunság National Park (KNP) in central Hungary, from 1998 to 2000. Alkaline lakes with bare, flat shorelines and islands are natural nesting and feeding habitats of avocets at this location. The lakes vary in surface area from 2-3 ha to 500 ha and in depth from a few cm to a maximum of 1 m. These shallow lakes change considerably among years depending on winter and spring precipitation and the growth of vegetation. Thus, avocets did not use every site every year and fieldwork was concentrated in areas of high nesting density and good accessibility for researchers. In addition to the natural breeding sites, I also included artificial habitats, such as a drained fishpond and a reconstructed wetland because of the importance of these areas to avocet nesting. Fieldwork started in early May in 1998 and in mid-March in 1999 and 2000 and ended in mid-July in each year with occasional visits to the study sites until October. Fieldwork was conducted on a total of 265 days.

2.2.1.2. Nest searching, measurements, and monitoring

Nests were located by searching areas used by avocets for nesting. Every nest was numbered, marked and its location was recorded on a map. I recorded the type of substrate and vegetation and the distance of the nest to the nearest water. I measured the maximum length and maximum width of each egg using a vernier caliper. Finally, I floated the eggs in a cup of water to determine their stage of incubation. Floating the eggs is not harmful for embryo development (Alberico 1998). Modifying the egg immersion technique of Nol & Blokpoel (1983) I used the following scheme to infer the incubation stage of eggs:

- Stage 1: axis of maximum length of the egg is horizontal: 0-1 days,
- Stage 2: axis is tilted in ca. 45°: 2-6 days,
- Stage 3: axis tilted in 90° (egg is standing on sharp end on bottom of cup): 7-12 days,
- Stage 4: egg is floating but does not reach the water surface: 12-15 days,
- Stage 5: egg is floating on the water surface but is not tilted: 16-19 days,
- Stage 6: egg is floating tilted on water surface: 20-23 days.

If the incubation stage of eggs within a clutch differed, I used an average stage for that clutch. I estimated the date of the start of incubation and calculated the expected date of hatching by adding 23 days (average incubation period, Cramp & Simmons 1983) to the start of incubation. To decrease potential disturbance on avocets, I visited nests only three or four days prior to the expected date of hatching. Colony visits were limited to 1 h in cold weather and 0.5 h in warm weather.

2.2.1.3. Definition and determination of nest fates

A nest was considered successful, if at least one egg of the clutch hatched. If eggs disappeared from the nest before the expected hatching date, the nest was considered depredated. In ambiguous cases, I determined nest fates by the presence or absence of tiny eggshell fragments, which are characteristic of nests in which eggs hatched (Mabee 1997). A nest was considered depredated if all eggs were missing and there were no tiny eggshell fragments in the nest. Mammalian predators were identified by footprints on the ground, toothmarks on the eggshells, eggs crunched in the nest (yolk in the nest-cup), eggs dropped during carrying or by eggs incompletely buried near nests. Avian predators were identified when the eggshell remnants indicated that eggs were cracked from one side and their content was drawn out. I found such eggshell fragments in nests in which eggs were seen being eaten by Harriers (*Circus aeroginosus*).

Incubation period was defined as the number of days between the laying of the last egg (exclusive) to the hatching of the first chick (inclusive). Hatching period was given by the number of days between the day of hatching of the first chick (inclusive) and the day of hatching of the last chick (exclusive) within a clutch

2.2.1.4. Banding and measuring chicks

Colonies in which nests were hatching were searched for young chicks at least once per day. Chicks were considered belonging to the nest in which they were found. I restricted nest checks to early mornings when it was cold and chicks were more likely to be in the nest than later during the day, when they were often at the edge of the water closest to the nest. If chicks were found in a nest, they were covered with a piece of cloth to keep them warm and to prevent them from leaving the nest while I was handling chicks in other nests. Chicks in a brood were banded with two plastic bands of seven different colors (white, yellow, orange, red, blue, green, and black) and a metal band from the Hungarian Ornithological Society on their legs above the tarso-metatarsus. The two color bands and one metal band were placed on chicks in a brood-specific combination. The chicks were distinguished by attaching pieces of tape of four different colors (white, yellow, red, and black) on the middle section of the metal ring.

I took three body size measurements on as many chicks as was possible. First, the length of the culmen was measured to the nearest 0.1 mm with a vernier caliper from the edge of down feathers between the eyes to the tip of the bill. Second, tarso-metatarsus length was measured with a vernier caliper (± 0.5 mm) by bending the chicks' right leg at the intertarsal joint and the 'ankle' and measuring the distance between the extreme bending points. Finally, the mass (± 0.5 g) of chicks was measured to the nearest gram using a Pesola spring scale.

2.2.1.5. Monitoring broods

Brood movements were monitored by regularly locating avocet families near the nesting colony, on brood-leading routes and in the brood-rearing areas. Searches were conducted by using a telescope to find vigilant adults and counting and identifying their chicks. I attempted to cover all areas used by avocet broods at least once in three days. During observations I used mobile and stationary hunting blinds or a car as a mobile observation point. The observation distance was always chosen to be large enough to minimize disturbance on avocets and on birds of other species. I used territory mapping to determine the number of broods at any one site and the location of territories and composition of avocet broods occupying them were recorded on enlarged copies of 1:10000 habitat maps.

2.2.1.6. Definition of the fate of chicks and broods

A chick was defined as fledged if it was seen at or after age 35 days, when avocet young are able to fly. Broods were considered successful if at least one chick fledged from them. Chick carcasses were difficult to find and in most cases the death of the chicks was only inferred by their disappearance from the broods. A chick was considered dead if it was not seen on at least three consecutive observation occasions.

2.2.1.7. Sampling of food availability

To quantify territory quality, I estimated the abundance of potential food items available to chicks on the territory of as many broods as possible. The food items of avocet chicks in my study sites are mostly aquatic and semiaquatic waterbugs (*Heteroptera*: *Corixidae*, *Notonectidae* and *Gerridae*), and dragonfly larvae (*Odonata*: *Anisoptera* and *Zygoptera*), water beetle larvae (*Coleoptera*: *Dytiscidae*, *Gyrinidae*), chironomid larvae (*Chironomidae*) and annelid worms (*Oligochaeta*) to a smaller extent (E. Boros, B. Kiss & Sz. Lengyel unpubl. data).

Sampling of food availability was conducted once in 1998 and twice in 1999 and in 2000, when I collected samples from territories of early as well as late broods. Territories were selected for sampling only if the brood occupying the territory consisted of young (< 2 wk old) chicks and if the brood was observed on the same territory at least twice in 4-5 days. I used territory maps recorded one day before sampling to identify territories for sampling.

The exact sampling location was standardized either in the center (two-dimensional territories) or the middle point (linear territories), because chicks fed in the center of a territory more often than on its edges. After locating the approximate center of the territory, I pushed down a plastic cylinder (diameter: 0.45 m) open on both ends into the lake floor covered by ca. 3-4 cm of water, the water depth preferred by young chicks for feeding. Next all aquatic invertebrate organisms were collected from the water enclosed by the plastic cylinder using a sweepnet (mesh size 0.2 mm). Macroscopic (>0.5 mm) aquatic invertebrates were put in jars, selected from the debris on trays in the field station and preserved in 70% ethanol until they were identified in the laboratory several weeks later.

The abundance of invertebrates was calculated by dividing the total number of individuals collected in a sample by the volume (circumference of sampling cylinder multiplied by water depth) of water from which they were collected, and expressed as the number of organisms per liter water.

2.2.2. Variables and statistical analyses

2.2.2.1. Variables

Egg volume (cm^3) was estimated according to Hoyt (1979) as $V = K_VL*B^2$, where L is the maximum length (in cm), and B is the maximum breadth (in cm) of the egg and K_V corrects for variation in shape and was calculated as $K_V = 0.5236 – [0.5236 * 2(L/W)/100]$ after Coulson (1963). The average value of K_V for avocet eggs calculated this way was 0.509 (± S.D. 0.001; n = 1348), which was identical to the mean value given by Hoyt (1979) for this coefficient in 115 species of birds (0.509 ± 0.008).

Fresh egg mass can be calculated as $M = K_M*L*B^2$, where L and B are the length and breadth of the egg, respectively, and K_M is a species-specific mass coefficient (Hoyt 1979). I used egg length, width and mass data on 168 fresh avocet eggs to estimate the mass coefficient based on the equation: $K_M = M/L*B^2$. The average value of K_M was 0.505 ± 0.029 (n = 168 eggs), which was close to the average value reported by Hoyt (1979) for 26 bird species (0.548 ± 0.016). I used the calculated value to estimate the fresh mass of eggs that were found two or more days after the completion of the clutch. There was no difference between measured and calculated fresh egg mass values (measured: 31.09 ± 2.961 g, calculated: 31.14 ± 2.961 g, paired $t_{167} = 0.397$, $p = 0.6921$) or between values estimated for unmeasured fresh eggs (31.26 ± 2.100 g, n = 176 eggs) and values measured for fresh eggs (31.09 ± 2.961 g, n = 168 eggs) ($t_{342} = 0.610$, $p = 0.5423$).

Body size variables of chicks (tarsus length, culmen length, and body mass) were highly correlated, therefore, they were reduced into one variable by a principal component analysis (PCA). To quantify body condition of chicks, I used the residuals from a linear regression of body mass on tarsus length. This variable is important for precocial chicks because they rely on their body reserves for survival during the first days after hatch (Starck 1993). The residual body mass relative to the structural size of the chick traditionally has been used as an index of the amount of reserves available for the chick (Starck 1993). To avoid pseudoreplication, I averaged chick body sizes for broods and used broods as data points in most analyses. The deviations of body size indexes from averages for broods were used to quantify individual chick quality.

2.2.2.2. Rationale for analyses

Because avocets used different alkaline lakes for nesting in each year, the interaction between year and location could not be tested. Nevertheless, because the data were collected over three years and in several colonies each year, both temporal (between-year) and spatial (among-colony) differences could be examined separately in one-way analyses. To control for temporal and spatial variation, I used the following logic for analyses.

I first tested whether there was a difference among years in variables. If there was a difference, I controlled for these differences in further analyses by using the residuals obtained by a one-way analysis of variance in which the studied variable was the response variable and year was the main effect. If the year effect was not significant in the first step, I used the raw data in the next step.

Next I analyzed whether there was a difference in the reproductive parameter among colonies in a one-way analysis of variance. Colonies were defined as a nesting aggregation of five or more pairs which defended their nests from predators as a single functional unit. The scale of colonies was more suitable to test spatial variation than was the scale of the lakes because colonies were sometimes farther from each other within a single lake than they were between two neighboring lakes. If there was a difference among colonies, I applied one of two ways to avoid pseudoreplication. First, if the reproductive parameter was normally distributed within colonies, and there were enough data to estimate the means for every colony, I calculated the mean value and used colonies as separate data points in analyses. Alternatively, I calculated residual values for the variable, which were obtained by a one-way ANOVA in which the studied variable was the response variable and colony was the main effect. If there was no difference among colonies, I used the raw values for variables.

Pseudoreplication could also arise if some adults had more than one nest during a year or nested in more than one year of the study. Avocets are known to re-nest within the same breeding season if their first clutch fails early (Cramp & Simmons 1983). I avoided within-year pseudoreplication in one of two ways. For data collected in 1998 and 1999, I excluded colonies that were likely to contain replacement nests from the relevant analyses. Alternatively, in 2000, I excluded data from a large colony that was depredated early in the season and from which failed adults could re-nest later in the season. One color-banded adult was known to re-nest in both 1999 and 2000, with less than eight days between the loss of the first nest and the laying of the first egg in the second nest. Pseudoreplication among years was less likely than within-year pseudoreplication because only one of the marked adults that bred in at least one of the study years (n = 25) was observed to breed in more than one year. However, in some analyses I treated each year separately.

Parametric statistical tests were used only if the assumptions of such tests were met by the data. In other cases, I used data transformations or applied non-parametric tests. Means ± 1 S.D. are given throughout the text unless noted otherwise and means ± 1 S.E. are shown on graphs. Two-tailed statistical probabilities are reported.

2.3. RESULTS

2.3.1. Population sizes of avocets

The Hungarian population of avocets has been slightly increasing during the 1990s. In 1993, the population size was estimated at 350 breeding pairs (Boros & Szimuly 1993), whereas by 2000 the population size exceeded 500 pairs (this study, E. Boros, Gy. Szimuly, pers. comm.) (Figure 1.).

In Hungary, avocets usually nest in one large and several smaller sub-populations in relation to the availability of nesting habitats. The largest sub-population usually breeds in southern Hungary, and most recently in the KNP (Figure 1.).

Avocet nests were found and monitored in nine localities during the three years of this study (Figure 2., Table 1.). Nesting occurred in each year at only two sites (Kelemen-szék and Zab-szék), whereas it occurred in two years at three sites, and in only one year in four of the sites. All but one site were located within a circle of 20 km in diameter (Figure 2.).

2.3.2. Biology of the nesting phase

2.3.2.1. Nesting chronology and colony formation

Avocets arrived back from the wintering grounds around March 5 in each study year. Avocets arrived in flocks and fed and loafed in flocks for a few weeks after arrival. Pre-breeding flocks usually consisted of 50-60 birds, with a maximum of 85 birds in one flock (Böddi-szék, March 31, 2000). Although some pairs appeared to be established upon arrival, most pairs were formed on the breeding grounds. During pair formation, aggressive displays among avocets were very frequent. Most pairs were formed by late March and early April. At this stage, pairs of avocets made long reconnaissance flights among the alkaline lakes, landing and gathering around potential nesting sites (mostly islands). Pairs appeared to probe potential nesting sites by feeding in the water near them and by going to the land to look for possible nest sites. After several pairs settled at a location, they conducted lengthy territorial fights both in the water and on the island, probably for small feeding territories and nesting sites. The first few pairs built their nests and laid their eggs simultaneously. Other pairs followed them and the number of nests quickly increased afterwards, which led to a high synchrony of nests within each colony.

I found and monitored 848 avocet nests (Table 1.), 95.6% of which were in colonies. These nests belonged to 33 colonies, of which 22 formed on islands and 11 were on the mainland, mostly on peninsulas. Overall, 82.3% of the nests (n = 848) were initiated on islands and 17.7% were started on the mainland. Island colonies were larger (31.0 ± 24.90 nests) than were mainland colonies (9.9 ± 6.80 nests) (Mann-Whitney U = 31.5, n = 33, p = 0.0006). In the island colonies nests could be as close to one another as 0.4 m, whereas in mainland colonies the minimum distance between nests was always larger than 5-6 m, and the maximum could be up to 30-40 m between neighboring nests. Six colonies were initiated in artificial habitats (drained fishpond and reconstructed wetland) and 27 colonies were in natural habitats (alkaline lakes). In spite of their overall tendency to nest in colonies, some avocets nested solitarily each year. Sixty-two percent of the solitary nests (n = 37) were built on the mainland, whereas 14 solitary nests were on small, and often remote, islands. Solitary nests were initiated on average 7.4 ± 18.45 days (n = 36 nests) after the annual mean laying date, whereas nests in colonies were started 0.4 ± 15.54 days (n = 705) before the average annual laying date (Mann-Whitney U = 9573.0, p = 0.0128). Solitary nests were more frequent in the latter part of the breeding season; solitary nests made up 3% of the nests initiated before the peak laying date and 7% of the nests were solitary after this date (n = 741 nests with known laying date, Fisher's exact p = 0.0161).

2.3.2.2. Nests, eggs and incubation

Nests were simple scrapes on the ground lined with dry grasses, twigs, aquatic plants, mollusk shells or mammalian droppings. The amount of materials used in the nest varied from almost none to quite a large amount and the height of the rim could be as high as 10 cm. Moreover, avocets were able to build their nests up to 15-20 cm high on an island threatened by flooding.

The mean julian date of initiation of first nests differed among years (Table 2.) and depended on weather in late March and early April. The earliest date of egg-laying occurred in 1999, however, on average, nests were initiated somewhat earlier in 2000 than in 1999 (Table 2., Tukey-Kramer $q = 5.86$, $q_{crit} = 2.91$, $p < 0.05$), and a month earlier in both years than in 1998 (Tukey-Kramer $q > 19.05$, $q_{crit} < 3.51$, $p < 0.05$ for both comparisons), when the spring was especially cold. The julian date of laying of individual clutches also differed significantly by colony when the among-year differences in laying dates were accounted for by using the residual laying date ($F_{18,371} = 30.086$, $p < 0.0001$).

Among the nests that were known to be complete ($n = 597$), 84.9% contained four eggs, 10.9% had three eggs, and 1.3% had two eggs. Clutches larger than four (superclutches) are usually combined nests in which two females lay their eggs (Hötker 2000). Superclutches were found in dense island colonies, and 2.3% of the complete nests ($n = 597$) contained five eggs and two nests (0.3%) had six and seven eggs, respectively. Finally, one nest (0.2%) contained eight eggs, of which the second set of four eggs was known to be laid eight days later than the first set and the two sets of eggs could be distinguished by egg color and pattern. Because this clutch was very likely laid by two females, I considered these as two different nests in subsequent analyses.

The mean clutch size of completed first nests ($n = 433$) was 3.9 ± 0.49 eggs and was fairly constant each year (Table 2.). Clutch size was known for more than half of the nests in 19 colonies of first nests. There was no difference in clutch size among these colonies (ANOVA, $F_{18,371}$ = 1.207, p = 0.2520). However, clutch size decreased during the season when colonies in which replacement nests occurred were included (Figure 3.). This was because clutches in colonies without replacement nests were significantly larger (4.0 ± 0.10 eggs, n = 19 colonies) than in colonies that were likely to contain replacement nests (3.8 ± 0.18 eggs, n = 6 colonies) (t_{23} = 3.585, p = 0.0016). Colony size did not influence clutch size (R^2 = 0.0001, $F_{1,23}$ = 0.004, p = 0.9512). Finally, clutch size did not differ between colonial and solitary nests (solitary: 4.0 ± 0.39 eggs, n = 20 nests, colonial: 3.9 ± 0.49 eggs, n = 433 nests, Mann-Whitney U = 4239.5, p = 0.7989).

Avocet eggs were olive-brown to light green with darker spots scattered on the surface. The coloring and spot pattern of the eggs are highly conservative among eggs of the same female. The average length of eggs was 50.23 ± 2.082 mm, and their maximum breadth was 34.99 ± 1.012 mm on average (n = 1348 eggs). The mass of fresh eggs (eggs in nests before completion and/or in floating Stage 1) was 31.09 ± 2.961 g (n = 168 eggs). The average fresh egg mass estimated for incubated eggs by using the linear dimensions of the egg was 31.24 ± 2.294 (n = 463), which was not statistically different from the measured values of fresh egg mass (t_{629} = 0.686, p = 0.4929).

Both the average volume and mass of eggs in first nests varied significantly among years (Table 2.). Eggs were significantly larger in 1999 than they were in 1998 (volume: Tukey-Kramer q = -1.274, q_{crit} = 0.766, $p < 0.05$, mass: q = -1.272, q_{crit} = 0.775, $p < 0.05$), whereas egg sizes did not differ ($p > 0.05$) between 1998 and 2000 and between 1999 and 2000. There was no seasonal change in either egg size variable in any of the study years ($R^2 < 0.008$, $p > 0.4$ for n = 6 regression analyses).

Egg size data were available for more than half of the nests in 13 colonies (total n = 263 nests). Egg volume and fresh egg mass did not differ among these colonies even after controlling for differences among years (egg volume: $F_{12,249} = 0.554$, $p = 0.8887$, egg mass: $F_{12,249} = 1.162$, $p = 0.3079$).

Avocet eggs usually hatch after 23-24 days of incubation by both parents. In this study the date of the laying of the last egg and the hatching of the first chick was known in 85 instances (20.9% of hatched nests, n = 407). The length of the incubation period of these nests was 22.9 ± 1.19 days. Incubation periods did not differ among years (Table 2.) or among colonies ($F_{12,70} = 0.906$, $p = 0.5452$) and it did not change significantly during the season ($R^2 = 0.018$, $F_{1,83} = 1.539$, $p = 0.2183$).

2.3.2.3. Hatching success, and factors influencing hatching success

The fate of nests could be determined in 823 cases (97.1% of all nests, n = 848). Overall, the proportion of nests hatching at least one egg was 49.5% (n = 823). Hatching success of nests did not differ among years (Table 3.). Nests in artificial habitats were more likely to produce hatchlings (76.0%, n = 200) than were nests in natural habitats (40.9%, n = 623) (Fisher's exact probability < 0.0001). Colonial nests were more likely to hatch (50.6%, n = 790) than were solitary nests (21.2%, n = 33) (Fisher's $p = 0.0011$) and nests in island colonies were more likely to hatch (57.7%, n = 667) than were nests in mainland colonies (12.2%, n = 123) (Fisher's $p < 0.0001$).

The proportion of successful colonies (in which at least one nest was successful) did not differ between years (Table 3.). However, the proportion of nests producing chicks in successful colonies showed significant annual variation (Table 3.). This was because in 1999 many nests were depredated in several colonies during incubation, and only few nests hatched young in these colonies. The proportion of successful nests within colonies decreased significantly during the season after controlling for the among-year variation (Figure 4.). This was because the residuals of the proportion of hatched nests differed between colonies started earlier than the annual peak laying date (5.4 ± 22.58%, n = 18) and colonies started after this date (-19.4 ± 25.72%, n = 5) (t_{21} = 2.107, p = 0.0473). A higher proportion of clutches hatched in colonies of 10 or more pairs (62.6 ± 27.7%, n = 19) than in colonies of fewer than 10 pairs (20.6 ± 13.6%, n = 4) (Mann-Whitney U = 11.0, p = 0.0284).

The hatching of all eggs in a nest usually took one or two days. The duration of hatching was known in 364 cases (89.4% of hatched nests, n = 407). In 46.7% of these cases, hatching took two days, whereas all eggs hatched on the same day in 35.7% of the cases. In 16.2% of the cases hatching lasted for three days, and in five cases (1.4%) chicks hatched over a period of four days. The duration of the hatching period was positively correlated with the number of chicks hatched per nest (Spearman r = 0.472, n = 358, $p < 0.0001$).

The exact number of hatched young was known in 390 cases (95.8% of hatched nests, n = 407). On average, 3.5 ± 0.82 chicks (range: 1 – 5) hatched in these nests. All four eggs hatched in 73.6% of the 4-egg nests (n = 371), three hatched in 17.3% of the cases, whereas two eggs hatched in 6.5% of the nests and only one of the four eggs hatched in 10 nests (2.7%).

The number, and proportion, of young hatched per nest did not differ among years (Table 3.). The proportion of young hatched per nest, however, differed among colonies ($F_{15,338}$ = 3.590, $p < 0.0001$). The proportion of hatched eggs per nest, averaged over colonies, ranged from 69.6% to 98.1%, and the low values were from colonies in which nests were partially depredated. After controlling for differences among colonies by using average values for each colony there was no seasonal trend in the proportion of hatched young per nest (R^2 = 0.0002, $F_{1,352}$ = 0.071, p = 0.7906). Colony size also did not influence the average proportion of hatched young per nest (R^2 = 0.005, $F_{1,14}$ = 0.069, p = 0.7961).

2.3.2.4. Failures of eggs and nests

More than half (50.5%) of the nests of known fate (n = 823) produced no hatchlings. Unsuccessful nests tended to be solitary nests (26 of 33 nests disappeared before the expected hatching date) and nests in mainland colonies (108 of 123 nests failed). Six of the nine colonies producing no hatchlings (n = 149 nests) were on the mainland. Two of the three failed island colonies (n = 96 nests) were close (<40 m) to the shoreline, and were depredated by terrestrial predators.

The cause of failure could be determined or inferred for 97.6% of the nests (n = 416). Eggs in the majority (88.4%) of the failed nests were taken by predators. Parents abandoned 10.1% of the failed nests, and 6 nests (1.5%) were flooded.

When eggs from a nest disappeared, usually all eggs were taken by the predators. However, in some large colonies, I also observed partial egg losses from nests. Ground predators (red foxes *Vulpes vulpes*, and badgers *Meles meles*) were found to revisit colonies that had already been partially depredated. For example, one or more red foxes visited a colony of 89 nests almost every other day in April 2000, and regularly took eggs from several nests, which resulted in all nests being depredated in two weeks.

The identity of predators could be determined in 77.7% of the depredated nests (n = 359). Mammals (red foxes and badgers) were responsible for the loss of eggs in 81.4% of the nests (n = 279). The rest (18.6%) of the depredated nests were destroyed by avian predators, mostly Harriers (*Circus aeroginosus*), which also were observed eating avocet eggs on three occasions.

2.3.2.5. Nesting phase - a summary

In summary, the effect of year was significant on laying date, egg size and colony hatching rate. Colonies differed in laying date, nest hatching success and proportion of young hatched per nest (Table 4.). Seasonal differences could be detected in clutch size and hatching rate within colonies

(Table 4.). Nests that were most likely to hatch were those in early island colonies of more than 10 pairs in artificial habitats.

2.3.3. Biology of the chick-rearing stage

2.3.3.1. Chick body size and body condition

The average culmen length of chicks less than 24 hours old was 15.6 ± 0.88 mm (range 13.0 – 19.5 mm, n = 602 chicks), their average tarsus length was 33.3 ± 1.42 mm (29.0 – 37.5 mm, 602 chicks), whereas their average body mass was 22.6 ± 1.79 g (16.0 – 27.5 g, 598 chicks).

The tarsus length of chicks younger than 24 hours was significantly correlated with both culmen length ($r = 0.424$, $n = 602$, Bonferroni adjusted $p = 0.0003$) and body mass ($r = 0.322$, $n = 598$, $p = 0.0003$). However, no significant relationship between culmen length and body mass was detected ($r = 0.072$, $n = 598$, $p = 0.0790$). Because of the interrelatedness of body size variables, I computed body size scores in a principal component analysis. The body size factor (PC1) explained 52.8% of the total variance of the three body size variables and it was positively correlated with each of the original body size variables of chicks younger than 24 hours ($r > 0.757$, Bonferroni-adjusted $p = 0.0003$ for each of the three comparisons). The average body size of chicks within a brood positively correlated with the average size of eggs in the nest (Table 5.). The order in which chicks hatched also significantly influenced their body size (Figure 5.); first-hatched chicks were significantly larger than fourth-hatched chicks. First-hatched chicks had longer tarsi ($F_{1,256} = 2.905$, $p = 0.0353$) and higher body mass ($F_{1,252} = 4.024$, $p = 0.0080$) than fourth-hatching chicks. The effect of hatching order on chick body condition was not statistically significant (Figure 6.).

The annual variation in body size variables was significant for tarsus length, whereas culmen length and body mass did not differ among years (Table 6.). Chick body size (PC1) and body condition were also not different among years (Table 6.).

Data on the body size of chicks were available in the majority of the broods in 15 colonies (62.5% of successful colonies, n = 24). The average body size within broods differed by colony ($F_{1,235} = 1.857$, $p = 0.0319$), whereas chick body condition was similar across colonies ($F_{1,235} = 0.986$, $p = 0.4678$).

The average body size of chicks within colonies decreased during the season (Figure 7.), whereas chick condition did not change with season ($R^2 = 0.142$, $F_{1,13} = 2.154$, $p = 0.1660$). Finally, neither body size nor condition was related to colony size ($0.224 <$ Spearman $r < 0.371$, $p > 0.1645$).

In summary, the body size of chicks differed among colonies because chicks were larger in earlier colonies than in late colonies. Within individual broods, egg size and chick body size were positively correlated, and first-hatched chicks were larger than last-hatched chicks.

2.3.3.2. Brood movement and the territorial system of broods

I monitored 367 broods or 90.2% of the 407 nests known to hatch in this study (Akasztói halastó: 95, Bába-szék: 9, Fehér-szék: 57, Kelemen-szék: 193 and Zab-szék: 13 broods).

Parents called their young away from the nest within a day of hatching of the last chick and led them to brood-rearing areas. The route taken and the distance travelled by the broods from the nesting sites to the feeding grounds depended on habitat quality and geographical features. At the natural nesting sites of alkaline lakes (Kelemen-szék, Zab-szék), the broods swam to the shore and moved along the shoreline (Figure 8.A). Broods that hatched in artificial habitats (e.g. drained fishpond near Akasztó, reconstructed wetland at Fehér-szék) almost invariably left the nesting pond to move to alkaline lakes (Figure 8.B). Brood-rearing areas were sometimes several kilometers away from the nesting sites and the broods often stopped and occupied territories temporarily (1-2 days) before crossing geographical obstacles (e.g. roads, reed-beds).

I identified 15 brood-rearing areas, which were used by broods for several weeks throughout the season. Most of these areas (n = 8) were used only in one year of the study, whereas five sites were used in two years and two sites were used in each of the three years.

Two kinds of spatial pattern of territories could be distinguished. Along bare shorelines the parents defended linear territories from one or two neighboring broods. In contrast, territories were usually two-dimensional in drying lakebeds, and any brood was likely to have two or more neighbors. The size of the territories was similar accross brood-rearing areas, and territories were more or less stable on a time scale of days. The factors influencing the location, size and shape of territories were the activity of brood members, spatial or temporal variation in food supply, changes in water level, and occupation of neighboring areas by other broods. Territorial fights between adults were frequent and usually resulted in one of the broods shifting its territory. Young downy chicks were observed to cross territory boundaries, but after 1-2 weeks adults attacked wandering chicks by pecking at them, swooping on them from the air, stepping on them and giving alarm vocalizations.

The main activity of adults with chicks was vigilance, during which they watched for predators in an upright posture. If adults noticed a predator, they mobbed and attacked it by diving on the predator while giving alarm calls. Other parental behaviors included brooding, leading the chicks, territorial defense; whereas self-maintenance behaviors were feeding, resting and preening.

2.3.3.3. Chick behavior and development

In the feeding grounds, young chicks spent most of the daylight hours feeding in shallow water and less time loafing or preening on the shoreline. Downy chicks usually spent the night and colder periods being brooded by their parents. Avocet chicks were brooded until they were 10 to 14 days old, after which brooding occurred only during extremely cold weather. Chicks within a brood showed a remarkably high synchrony in their behavior. During predator attacks the downy chicks usually crouched and depended on their camouflage plumage to avoid predation, whereas chicks older than two weeks post-hatch actively ran for vegetation cover upon the alarm calls of their parents.

The first white feathers occurred in the wing and the belly area of the chicks just before two weeks of age. At three weeks, chicks were mostly white and their main activity was still feeding. The chicks reached the overall size of their parents by the fourth or fifth week. Chicks at this age spent most of their time resting and preening.

Fledging usually occurred at 30-35 days post-hatch, although I observed young capable of flying at 28 days of age. Fledged juveniles usually aggregated in groups, mostly with their parents. These groups would move around among the alkaline lakes or stay on the natal lake for several weeks. The break-up of the family unit occurred several weeks after fledging, however, some broods stayed together during pre-migration movements. By late July, most adults had left the breeding grounds. The juveniles often aggregated in large flocks in July-August, and sometimes stayed at the alkaline lakes as late as October. In most years, both adult and juvenile avocets from several breeding sites gathered in one area in southeastern Hungary. The last observation of avocets at the study sites was October 25 in 1998, November 20 in 1999 and December 10 in 2000.

2.3.3.4. Fledging success and the factors influencing fledging success

2.3.3.4.1. Fledging success of chicks

Chick fate (survived/died) could be determined for 90.1% of the chicks known to hatch (n = 1301). Of the 1172 chicks whose fate was known, 309 (26.4%) fledged. A significantly higher proportion of chicks fledged in 1999 and 2000 than in 1998 (Table 7.). Similarly, the number, and the proportion, of chicks fledged per brood was lowest in 1998 and higher in 1999 and 2000 (Table 7.). The proportion of broods fledging chicks was also higher in 1999 and 2000 than in 1998, whereas the number and proportion of fledged chicks in successful broods did not differ among the years (Table 7.).

The mortality of chicks was highest during the first week post-hatch, when more than half of the chicks disappeared in each study year (Figure 9.). The percentage of chicks surviving until one week of age per brood was 37.5%, whereas 29.9% survived until two weeks and 25.6% survived until three weeks of age. Mortality after three weeks post-hatch was rare (Figure 9.).

The order in which chicks hatched did not influence whether or not chicks fledged (G = 4.347, df = 3, n = 426, p = 0.2264). The proportion of fledged young varied between a high of 26.3% for first-hatched chicks and a low of 16.8% for third-hatched chicks. The residual body size (which was independent of the brood mean) of newly hatched chicks did not influence whether or not they fledged (logistic regression, R^2 = 0.001, n = 576, p = 0.3774). The effect of residual chick body condition on fledging success also was non-significant (logistic regression, R^2 = 0.0002, n = 572, p = 0.7010).

2.3.3.4.2. Fledging success of broods

The fate of broods was known for 340 broods (92.6% of 367 broods total). Nine broods ceased to function because chicks died in the nest (4 cases), were adopted by other broods (4 cases) or were abandoned by the parents (1 case). At least one chick fledged from 154 (46.5%) of the remaining broods (n = 331), whereas 53.5% of the broods failed to fledge any young. In eight broods only adopted chicks fledged. Four chicks fledged in only seven broods (4.8% of the broods fledging at least one natal chick, n = 146), whereas three chicks fledged in 23 broods (15.8%), two chicks fledged in 53 broods (36.3%) and one chick fledged in 63 broods (43.2%).

The number of young fledged per brood differed both by year (Table 7., two-way ANOVA on log-transformed data, $F_{2,166} = 6.127$, $p = 0.0027$) and brood-rearing location ($F_{14,166} = 2.662$, $p = 0.0016$), whereas the interaction between year and location was not significant ($F_{4,166} = 1.462$, $p = 0.2162$). The proportion of chicks fledged per brood also differed among years (Table 7., $F_{2,162} = 10.671$, $p = 0.0001$) and locations ($F_{14,162} = 3.992$, $p = 0.0001$), whereas the interaction of year and location was not significant ($F_{4,162} = 0.251$, $p = 0.9088$). The cause of the among-year variation was that fledging success was low in 1998 and high in 1999 and 2000 (Table 7.). Fledging success varied among brood-rearing locations between 7% to 70% of the chicks fledging per brood. The spatial variation in fledging success was caused mainly by a difference between natural and artificial habitats. In 1998 and 1999, when nesting occurred in both natural and artificial habitats, 68.2% of the broods in natural habitats (n = 66) fledged chicks, whereas only 30.2% of the broods in artificial habitats (n = 126) were successful (Fisher's $p < 0.0001$). Pairs in natural habitats (n = 66) fledged 1.2 ± 1.15 or 47.6 ± 40.56% of their chicks, whereas pairs in artificial habitats (n = 126) fledged 0.5 ± 0.94 or 16.1 ± 28.41% of their chicks (Mann-Whitney-test, number of fledged young: $U = 9731.5$, $p < 0.0001$, proportion of fledged young: $U = 9430.0$, $p < 0.0001$). The reason for this difference was that pairs nesting in artificial habitats moved their broods to natural habitats (alkaline lakes) by traveling several kilometers on land, which caused high mortality among young chicks for two reasons. First, chicks were exposed to both aerial and terrestrial predators. Second, single pairs could not defend their chicks from predators effectively, because avocets rely on mobbing by many individuals to deter predators.

Pairs that laid their eggs earlier were more likely to fledge chicks than pairs laying later when differences in laying dates caused by year and colony were controlled for (logistic regression, $R^2 = 0.02$, $\chi^2 = 6.949$, n = 315, p = 0.0084).

Brood size was also important in the probability of producing fledglings. More than half of the broods with three or more chicks fledged young, whereas less than half of the broods with one or two chicks did so, both in the low predation years (1999 and 2000) (Table 8., G = 11.516, df = 4, p = 0.0213) and in all years combined (G = 15.493, df = 4, p = 0.0038). There were not enough data to test the high predation year of 1998 separately (Table 8.). However, brood success did not differ by brood size when data from 1998 were grouped by brood size because 14.3% of the broods with one or two chicks (n = 14 broods) fledged young, and 32.1% of the broods with three or more chicks (n = 28) fledged young (Table 8., Fisher's p = 0.2826).

Brood size also significantly influenced the number of chicks fledged per brood both when data from all years were combined (Figure 10., Kruskal-Wallis H = 21.501, df = 4, p = 0.0003) and when only the years of low predation (1999 and 2000) were included (Figure 10., Kruskal-Wallis H = 18.030, df = 4, p = 0.0012). There was no difference in the number of young fledged by brood size in the high predation year of 1998 (Kruskal-Wallis H = 5.496, df = 4, p = 0.2401).

After controlling for annual differences in the abundance of aquatic macroinvertebrates (B. Kiss & Sz. Lengyel, unpubl. data), prey density positively influenced whether the brood occupying the territory was successful or not (logistic regression, $R^2 = 0.124$, n = 63, p = 0.0141). The number of fledged young was positively correlated with prey density (r = 0.461, n = 63, p = 0.0001), in part because larger broods occupied territories with higher prey density (r = 0.355, n = 63, p = 0.0040) and had a higher fledging success than smaller broods (Figure 10.).

Broods from solitary and colonial nests were equally likely to fledge chicks (solitary: 50%, n = 10 broods, colonial: 45.0%, n = 313, Fisher's exact p = 0.7594) and there was no difference in the average number of chicks fledged between solitary and colonial broods (solitary: 1.4 ± 1.65 chicks, n = 10, colonial: 0.8 ± 1.06 chicks, n = 313) (Mann-Whitney U = 1296.0, p = 0.3078). There was no correlation between the number of broods at a given brood-rearing site and the average proportion of young fledged per brood (r = 0.145, n = 12, p = 0.6624).

The average body size of chicks in a brood did not influence whether the brood produced fledglings or not (logistic regression, $R^2 = 0.002$, $\chi^2 = 0.501$, n = 242 broods, p = 0.4790). Similarly, the body condition of chicks did not affect brood success (logistic regression, $R^2 = 0.003$, $\chi^2 = 0.866$, n = 242, p = 0.3522). These results were similar (p > 0.48) in both the high predation year (1998) and the low predation years (1999-2000).

In summary, fledging success was lower in 1998 than it was in 1999 and 2000, and it was influenced by both season and habitat. Early broods were more likely fledge young than were late broods and more chicks survived in natural habitats than in artificial habitats where broods traveled on land to feeding areas. Larger broods occupied better territories than smaller broods, and brood size positively influenced the probability of fledging and the number of fledglings per brood. Within broods, neither hatching order nor chick body size influenced fledging success.

2.3.3.5. Causes of chick mortality

The exact causes of mortality of chicks could be determined only for chicks whose carcass or body parts were found (n = 75 chicks). In all other cases, mortality was inferred by the disappearance of chicks from their broods, and the cause of mortality was assumed to be predation. This probably overestimated predation on chicks because the carcasses of chicks that died from any other reason could disappear rapidly from the study areas. This was likely because chick carcasses usually lay on the ground with their white belly upwards, which made them conspicuous for scavengers.

Almost a third (30.7%) of the chicks whose carcass were found died from predation. In most cases, I found only the legs of chicks, which is a typical sign of predation by harriers. In cases when only the plastic or metal bands of chicks were found, the chicks were assumed to have died from mammalian predation. I found toothmarks on several plastic bands and live chicks rarely lost bands in this study (0.4% of 696 banded chicks were known to have lost bands).

Exposure caused the death of 17 chicks (22.7% of the carcasses). These carcasses were found wet and stuck in the mud after storms. Inclement weather, however, also may have caused mortality indirectly by reducing the time chicks spent feeding. During bad weather the chicks were brooded almost continuously by their parents. Chicks that were prevented from feeding by bad weather also may have been weaker and more susceptible to predation.

In mixed-species colonies, young chicks occasionally were killed by gulls and terns, which were aggressive toward young avocet chicks passing by their nests. Twenty percent of the chick carcasses had wounds on their head, a sign of the chick having been hit by gulls or terns.

In 11 cases (14.7%), the freshly hatched chicks showed developmental abnormalities such as poor ability to walk arising from weak or abnormally developed legs (nine chicks), and open yolk sacs (two cases). All of these chicks died in or near the nest. These chicks hatched from nests initiated late in the season or from nests that had more than the usual four eggs.

In two cases (2.7%), unbanded chicks got tangled in dry twigs and died. Finally, in seven cases (9.3%), it was not clear how the chick died and the cause of mortality was unknown.

2.3.4. Breeding success and population dynamics

2.3.4.1. Return rates and age at first breeding

Three (14.3%) of the 21 chicks fledged in 1998 were resighted at the study sites as first-year birds in 1999, and 23 (14.5%) of the 159 chicks fledged in 1999 were resighted in 2000. In 1999 two (66.7%) of the three returned yearlings were known to breed, whereas in 2000 the nesting of 13 (56.5%) of the returning yearlings (n = 23) was confirmed. One bird banded as a chick in 1998 returned in both 1999 and 2000, and was known to nest (unsuccessfully) in both years. Interestingly, this bird nested in 1999 at the same site (± 10 m) where it had been reared by its parents in 1998. In all, 57.7% of the first-year birds returning to the study sites (n = 26) were confirmed to breed.

2.3.4.2. Breeding success, recruitment and population dynamics

Breeding success varied considerably within the three years of this study (Table 9.). While hatching success was relatively high and did not vary among years (Table 3.), fledging success was low and varied among the years (Table 7.).

Assuming a return rate of 14% and a yearling breeding rate of 57% (see above), recruitment in 1999 from 1998 is calculated to be 1.7 breeding adults. This recruitment rate does not explain the increase in the number of breeding pairs between 1998 and 1999, which was more likely a result of immigration of individuals from other areas. For example, two adults bred on Kelemen-szék in 1999 that had been banded as chicks in Donana National Park in southwestern Spain (ca. 3500 km). The recruitment from 1999 in 2000, assuming the same return rate and proportion of yearling breeders, was 12.7 breeding individuals. One individual from 1998 returned and bred in both 1999 and 2000, but no other individual from the 1998 cohort was seen returning in 2000. Assuming a 90% adult yearly survival rate (Cadbury & Olney 1978), the recruitment from 1999 to 2000 was probably still too low to compensate for mortality or emigration of adults (27 pairs or 54 individuals). These calculations indicate that the maintenance of the population at the current levels (>200 pairs) is unlikely without the immigration of individuals from other populations.

2.4. DISCUSSION

This study provides several important findings about colonial nesting and the factors influencing breeding success in the largest inland population of avocets in Europe. First, both spatial and temporal characteristics of nesting influence the chance of hatching. Spatial characteristics are important because 96% of the pairs nest in colonies and 82% of the pairs nest on islands. The tendency to nest in colonies is strong in avocets, and is shown by the fact that nests are started earlier in colonies than solitarily. Alternatively, the limited availability of suitable nesting habitats may force pairs to nest in close proximity. This effect may explain the formation of dense colonies in dry years, such as in 1998, when islands are not scarcely available. However, the tendency to nest in colonies appears to be more important than habitat availability because in the wet years of 1999 and 2000 some colonies that were started approximately at the same time were on the mainland and some, apparently suitable, islands were avoided. Solitary nests occur more frequently later in the season, probably because some young and/or inexperienced breeders can not establish themselves in the colonies. Nests in colonies have a higher chance of hatching eggs than do solitary nests and colonies in artificial habitats are more successful than colonies in natural habitats. Hatching success is higher in island colonies than in mainland colonies.

The temporal characteristics of nesting are also important, because clutches in colonies established earlier are larger and more likely to hatch than nests in late colonies. Chicks hatching in early colonies are generally larger than chicks hatching in late colonies. One probable reason for these seasonal differences is that late colonies are likely to contain replacement nests and potentially contain nests of young and inexperienced breeders.

The most important cause of nest and egg loss is predation and the differences in hatching success can be explained by the spatial distribution of different kinds of predators. Colonies provide protection against aerial predators because nesting adults mob and attack predators. The number of pairs, therefore, can be important and this may explain why colonies of more than 10 pairs are more successful than are colonies of fewer than 10 pairs. The reason that artificial nesting sites and islands have higher hatching success is probably because ground predators (mammals) can not gain access to or avoid these areas. Predation by mammals is the main reason for egg loss in several other studies of avocets (Cadbury & Olney 1978; Watier & Fournier 1980; Cadbury et al. 1989; Girard & Yesou 1989; Hötker 2000). Indeed, hatching success in the Hungarian avocet population was similar to that found in coastal populations (Table 10.).

Fledging success also shows spatial and temporal variation. Fledging success is higher in natural brood-rearing locations than in artificial habitats because chick mortality is high during movements of broods from artificial nesting habitats to brood-rearing locations in natural areas. Temporal differences also exist because broods that hatch earlier in the season are more likely to be successful than are broods hatching later in the season.

The most important factor in chick mortality appeared to be predation, based on the small number of chick carcasses found in this study. Several indirect observations provide further evidence for the importance of predation. First, most chick mortality occurs during the movement of broods to feeding areas on land, when and where they are highly vulnerable to predators.

Second, chick survival is lower later in the breeding season, when the emergence of the young of several predators (e.g. foxes, badgers, harriers) increases predation pressure. Finally, larger broods are more likely to fledge chicks, and fledge more chicks, than do smaller broods, indicating that brood success is density-dependent. Density-dependent mortality is compatible with the predation explanation but not with the weather explanation of brood success. The positive relationship between brood size and fledging success found in this study are in contrast with those of Safriel (1975) who found that in the Semipalmated Sandpiper (*Calidris pusilla*) larger broods are more likely to become completely depredated than are smaller broods.

Variation in the breeding success of avocets mostly is determined by variation in fledging success and is less affected by variation in egg hatching success. This result has been found in several other studies of avocets. For example, in the Wadden See area of northern Germany, the major determinant of variation in breeding success is chick survival, which in turn appears to be related to annual June temperatures (Hötker & Segebade 2000). On the Atlantic coast of France even in good years, only a few chicks fledge in successfully hatching colonies of up to 400 pairs (Hagemeijer & Blair 1997). Finally, chick loss is the most important factor in explaining the total annual losses of avocets in England between 1947 and 1986 (Hill 1988). The breeding success of the Hungarian population was within the range reported for avocets breeding in coastal areas (0.1 – 3.0 fledged chicks per pair, Hötker & Segebade 2000).

The observation that more than half of the yearlings returning to my study sites bred contradicts reports in the literature that indicate two years as the age at first breeding in avocets (Cadbury & Olney 1978; Cramp & Simmons 1983). Although future studies are necessary to explore the link between breeding success and the changes in population size, it appears that the growth of the Kiskunság population is unlikely to be due to recruitment from within the population.

Two ecological reasons can be proposed to explain the increase in population size. First, the size of the Hungarian population may undergo long-term fluctuations in relation to wetter and drier weather periods. Indeed, in the extremely dry years of 1985 and 1992 fewer than 10 pairs bred at the alkaline lakes, the main natural habitat of avocets in Hungary (Boros & Szimuly 1993). The number of pairs breeding at these lakes increased considerably between 1995 and 2000 (Figure 1.), during which period the years became progressively wetter. Higher levels of spring precipitation increased water levels in the lakes, leading to longer shorelines and more islands, which in turn increased the availability of nesting sites for avocets. The higher availability of nesting sites appears to have coincided with an influx of individuals from coastal populations. This was supported by two individuals that were banded as chicks in southwestern Spain and bred in central Hungary in 1999. Second, the increase in population size also can be explained by a higher availability of artificial nesting habitats in Hungary and in Europe in general (Hagemeijer & Blair 1997). Artificial habitats in Hungary include dike systems for rice fields, goose farms, wastewater treatment ponds and drained fishponds. Breeding success in such habitats is usually lower than that in natural ones (this study, E. Boros, Gy. Szimuly pers. comm.).

The spatial variation in breeding success has conservation implications. Hatching success is higher in artificial than in natural habitats whereas fledging success is higher in natural than in artificial areas. These results suggest that avocets may not correctly assess the chances of successful reproduction (habitat mal-assessment hypothesis, Székely 1992). Therefore, conservation efforts should concentrate on preserving natural habitats rather than on creating new habitats.

In conclusion, colonial nesting, habitat type and timing of breeding each is correlated to the breeding success of avocets. Variation in fledging success has the largest influence on variation in breeding success, and fledging success is highest for early broods in natural habitats. This finding emphasizes the conservation importance of such habitats.

2.5. TABLES

Table 1. Number of nests and colonies by year and study site. A colony was defined as the nesting aggregation of at least five pairs that reacted the same way to approaching predators.

Year	**Study lake**	**Number of nests**	**Number of colonies**
1998	Böddi-szék	5	0
	Cserebökény	11	1
	Fehér-szék	49	2
	Kelemen-szék	32	3
	Zab-szék	41	2
1999	Akasztói halastó	119	3
	Bába-szék	25	1
	Böddi-szék	8	1
	Fehér-szék	35	1
	Kelemen-szék	130	6
	Zab-szék	3	0
2000	Bába-szék	89	1
	Csaba-szék	55	3
	Kelemen-szék	194	7
	Zab-szék	40	1
	Kerek-rét	12	1
Total		848	33

Table 2. Nesting parameters in the three years of the study. Sample sizes are in parentheses. Clutch size is shown for nests that were known to be complete. Egg size variables were averaged for each nest, and sample size is number of nests.

Variable	**1998**	**1999**	**2000**	**F***	**df**	**p**
Number of nests	138	320	390			
Number of breeding pairs [a]	110	274	301			
Earliest date of egg-laying	28 April	27 March	31 March			
Julian date of nest initiation [b]	59.0 ± 12.14 (115)	39.9 ± 14.48 (237)	34.1 ± 9.43 (175)	144.83	524	< 0.0001
Clutch size	3.9 ± 0.63 (82)	3.9 ± 0.48 (211)	4.0 ± 0.40 (140)	0.21	430	0.8149
Egg volume, cm^3	30.56 ± 2.201 (65)	31.83 ± 2.071 (105)	31.29 ± 1.914 (89)	7.76	256	0.0005
Fresh egg mass, g	30.66 ± 2.189 (65)	31.93 ± 2.090 (105)	31.26 ± 1.980 (89)	7.74	256	0.0005
Incubation period, days	23.3 ± 1.31 (25)	22.8 ± 1.06 (34)	22.7 ± 1.16 (26)	2.25	82	0.1120

[a] The number of breeding pairs was estimated by subtracting the number of potential replacement nests from the total number of nests within a year.

[b] Julian dates are given as days after March 15 of each year.

* One-way ANOVA.

Table 3. Hatching success variables in the three years of the study. Successful colonies were those in which at least one nest was known to hatch (n = 23 colonies, n = 641 nests). In 1999, numerous nests in several colonies were depredated, which explains the high proportion of successful colonies, but the lowest colony hatching proportion in the three years.

Variable	**1998**	**1999**	**2000**	**Statistic***	**df**	**p**
Percentage of eggs hatched	56.9 (290)	56.3 (968)	58.1 (1009)	G = 0.646	2	0.7239
Percentage of nests hatched	43.5 (124)	53.3 (315)	48.2 (384)	G = 3.883	2	0.1435
Percentage of successful colonies	62.5 (8)	83.3 (12)	69.2 (13)	G = 1.226	2	0.5417
Percentage of hatched nests per successful colonies	57.1 ± 32.83 (4)	37.4 ± 28.06 (10)	74.3 ± 20.57 (9)	F = 4.730	20	0.0208
Number of hatched chicks per nest	3.4 ± 0.851 (50)	3.4 ± 0.804 (167)	3.5 ± 0.833 (173)	F = 0.618	387	0.5395
Percentage of eggs hatched per nest	87.7 ± 21.0 (50)	89.2 ± 18.5 (165)	89.1 ± 20.0 (172)	F = 0.123	384	0.8845

* G: G-test, F: one-way ANOVA

Table 4. Summary table of reproductive parameters during the nesting phase.

Variable	**Year effect**	**Colony effect**	**Seasonal effect**	**Difference**
Laying date	Yes	Yes	-	1. Spring weather influenced the start of laying. 2. Colonies were formed at different times in a season.
Clutch size	No	No	Yes	Early colonies had larger clutches than late colonies, which were likely to contain replacement nests.
Egg size	Yes	No	No	Eggs were largest in 1999, intermediate in 2000 and smallest in 1998.
Nest hatching success	No	Yes	-	1. Nests in artificial habitats were more successful than in natural habitats. 2. Colonial nests were more successful than solitary nests. 3. Island colonies were more successful than mainland ones.
Proportion of hatched nests per colony	Yes	-	Yes	1. Many colonies were partially depredated in 1999. 2. Earlier and larger colonies were more successful than later and smaller colonies.
Proportion of young hatched per nest	No	Yes	No	Fewer young hatched per nest in partially depredated colonies than in colonies not depredated.

Table 5. Correlation coefficients between egg size and chick body size variables. Body size (PC1) represents scores obtained by a principal component analysis of the three original variables of body size, whereas body condition index is the residual of body mass regressed against tarsus length. All variables were averaged for broods and one brood represents one datapoint in the analyses shown (n = 173 broods). Significance levels were adjusted for multiple comparisons by the sequential Bonferroni method. ns, non significant, * p < 0.005, **p < 0.0005

	Culmen length	**Tarsus length**	**Body mass**	**Body size (PC1)**	**Body condition index**
Egg volume	0.092 ns	0.254*	0.759**	0.464**	0.733**
Egg mass	0.086 ns	0.232*	0.718**	0.435**	0.696**

Table 6. Variables of body size of chicks in the three years of the study. Body size and the body condition index were obtained as given in **Table 5**. Sample sizes (number of broods) are given in parentheses. Significance values were adjusted for multiple comparisons by the sequential Bonferroni method.

Variable	1998	1999	2000	F*	p
Culmen length (mm)	15.2 ± 0.90 (27)	15.6 ± 0.76 (120)	15.6 ± 0.71 (115)	3.573	0.1180
Tarsus length (mm)	33.8 ± 1.26 (27)	33.4 ± 1.10 (120)	33.0 ± 1.16 (115)	7.646	0.0030
Body mass (g)	22.7 ± 1.45 (27)	22.9 ± 1.74 (119)	22.6 ± 1.51 (114)	1.498	0.5205
Body size (PC1)	-0.011 ± 0.960 (27)	0.114 ± 0.846 (119)	-0.098 ± 0.859 (114)	1.763	0.5205
Body condition index	-0.149 ± 1.173 (27)	0.195 ± 1.621 (119)	-0.003 ± 1.388 (114)	0.855	0.5205

* F: one-way ANOVA

Table 7. Fledging success variables in the three years of the study. Broods in which only adopted chicks survived (n = 8) were excluded from brood success calculations. Sample sizes are in parentheses.

Variable	1998	1999	2000	Statistic*	p
Percentage of fledged chicks	12.2 (172)	30.2 (520)	27.2 (481)	G = 24.766	< 0.0001
Number of chicks fledged per brood	0.35 ± 0.770 (51)	0.92 ± 1.122 (141)	0.90 ± 1.094 (131)	H = 13.497	0.0012
Percentage of chicks fledged per brood	11.3 ± 24.99 (51)	32.6 ± 38.03 (141)	29.5 ± 36.24 (131)	H = 14.587	0.0007
Percentage of broods fledging chicks	21.6 (51)	51.1 (141)	48.1 (131)	G = 14.794	0.0006
Number of fledged chicks in successful broods	1.64 ± 0.809 (11)	1.81 ± 0.929 (72)	1.87 ± 0.813 (63)	H = 1.191	0.5512
Percentage of chicks fledged in successful broods	52.3 ± 27.66 (11)	63.9 ± 28.74 (72)	61.3 ± 27.76 (63)	H = 1.600	0.4494

* G: G-test, H: Kruskal-Wallis test

Table 8. Number of successful broods (defined as producing at least one fledgling) as a function of brood size. Broods that were used for experiments (n = 118) are excluded.

		Number of chicks in brood				
Year	**Variable**	**One**	**Two**	**Three**	**Four**	**Five or more**
1998	Number of successful broods	0	2	2	5	2
	Number of unsuccessful broods	4	8	6	12	1
1999-2000	Number of successful broods	5	8	29	33	10
	Number of unsuccessful broods	11	13	17	18	3
Total		20	31	54	68	16

Table 9. Breeding success of avocets nesting in natural and artificial habitats in the three years of the study. Data were included only from areas in which nests and broods were closely monitored (n = 734 nests, 582 pairs). In 1998 and 1999 renesting occurred only in natural habitats, and in 2000 all known nests were in natural habitats.

	1998		**1999**		**2000**	
Variable	**Natural**	**Artificial**	**Natural**	**Artificial**	**Natural**	**Artificial**
Number of fledged chicks per number of nests	0.130	0.234	0.512	0.484	0.444	-
Number of fledged chicks per pair	0.200	0.234	0.716	0.484	0.636	-
Number of fledged chicks per successful nests	0.667	0.379	1.509	0.655	0.708	-

Table 10. Hatching success in studies of avocet populations in Europe. Hatching success is given as the number of hatched eggs divided by the number of eggs known. This table is based on Table 2. of Hötker & Segebade (2000).

Location	**Study years**	**Hatching success (%)**	**Number of nests**	**Reference**
Havergate, England	1947-1988	76	-	Cadbury & Olney 1978
Minsmere, England	1963-1988	47	-	Cadbury & Olney 1978
Oostvaardersplassen, Netherlands	1973, 1975	59	323	Bie & Zijlstra 1985
Marais d'Olonne, France	1976-79	42	1085	Watier & Fournier 1980
Marais d'Olonne, France	1977-1983	65	1471	Girard & Yesou 1989
Evros Delta, Greece	1980-81	81	-	Goutner 1985
Antwerpen-Linkeroever, Belgium	1982-1991	74	458	Van Impe 1991
Salina di Cervia, Italy	1983-85	77	28	Casini 1986
Nordfriesland, Germany	1988-1997	49	3505	Hötker & Segebade 2000[a]
Kiskunság, Hungary	1998-2000	57	579	This study [b]

[a] Hatching success was calculated by the Mayfield method (Mayfield 1961)

[b] Only the nests with known clutch sizes are included.

2.6. FIGURE LEGENDS AND FIGURES

Figure 1. Population sizes (number of pairs) of avocets breeding in the Kiskunság National Park (the main study site), and several sites in southern Hungary between 1995 and 2000. Data were collected by gathering information from people with knowledge of the breeding areas (1995, 1996), and by censusing the main breeding habitats of avocets in early spring of each year between 1997 and 2000.

Figure 2. The geographical distribution of Pied Avocets in Europe (A) and Hungary (B) and map of the study sites in central Hungary.

Figure 3. Mean clutch size per colony as a function of colony starting date. The annual variation in laying dates was controlled for by using the residuals from a one-way ANOVA of egg laying dates with year as the main factor. Colony starting date was defined as the minimum value of these residuals within a colony. Most colonies were started before the mean annual laying date (indicated by 0). Colonies likely to contain replacement nests are indicated by open circles. Colonies were included in the analysis if clutch size was known for more than 50% of the nests (clutch size was known for an average of 84.5 ± S.D. 14.59% of the nests in the 25 colonies shown). Linear regression, $R^2 = 0.275$, $F_{1,23} = 8.728$, $p = 0.0071$.

Figure 4. Proportion of nests hatched per colonies as a function of colony starting date. To control for annual variation in proportion of hatched nests per colony, residuals are shown from an ANOVA in which the proportion of hatched nests per colony was the response variable and year was the main factor. Colony starting date was defined as in Fig. 3. Colonies were included in this analysis if at least one nest hatched within the colony (n = 23 colonies). Open circles indicate colonies in which replacement nests may have occurred. Linear regression, $R^2 = 0.227$, $F_{1,21} = 6.161$, $p = 0.0216$).

Figure 5. Mean (± S.E.) body size of chicks as a function of hatching order. Chick body size was quantified as factor scores (PC1) from a principal component analysis of culmen length, tarsus length and body mass of chicks. Sample sizes are in parentheses. First-hatched chicks were significantly larger than fourth-hatched chicks (one-way ANOVA, $F_{3,252} = 3.074$, $p = 0.0283$, Tukey-Kramer $q = 0.500$, $q_{crit} = 0.448$, $p < 0.05$).

Figure 6. Mean (± S.E.) body condition of chicks as a function of hatching order. Chick body condition was measured by the residuals of a regression of body mass on tarsus length.. Sample sizes are in parentheses. The difference by hatching order was not statistically significant (one-way ANOVA, $F_{3,252} = 2.496$, $p = 0.0604$).

Figure 7. Chick body size averaged for colonies as a function of colony laying date. Chick body size (defined as in Fig. 5.) was averaged by colonies if it was available for at least 50% of the broods in the colony (chick body size was known for an average of 73.8 ± S.D. 18.40% of the broods in the n = 15 colonies shown). Colony laying date was the colony average of the residuals of laying dates obtained by a one-way ANOVA of laying dates with year as the main factor. Linear regression, $R^2 = 0.309$, $F_{1,13} = 5.825$, $p = 0.0313$.

Figure 8. Examples of brood movements in natural habitats (A, alkaline lake “Zab-szék”) and in artificial habitats (B, from reconstructed wetland “Fehér-szék”). In natural habitats (A) avocet broods swam to the shore from the island colony (indicated by X) and used the shorelines and drying lakebeds as feeding areas. From nesting islands in artificial nesting habitats (B) adult avocets led their young to feeding areas in natural habitats through land. Traveling on land caused high mortality among young chicks.

Figure 9. Chick survival as a function of age. Chicks were included in the analysis only if they were seen at least once after they left the nesting island (n = 98 chicks or 53.6% of all chicks known to hatch in 1998, 432 or 74.4% in 1999 and 401 or 74.7% in 2000). Mortality was highest in 1998, when 46.4% of the chicks known to hatch were not even seen after hatching. There was no chick mortality between 28 days of age and fledging (defined as 35 days).

Figure 10. Mean (± S.E.) number of young fledged per brood as a function of brood size in the three years of the study. Sample sizes (number of broods) are above bars.

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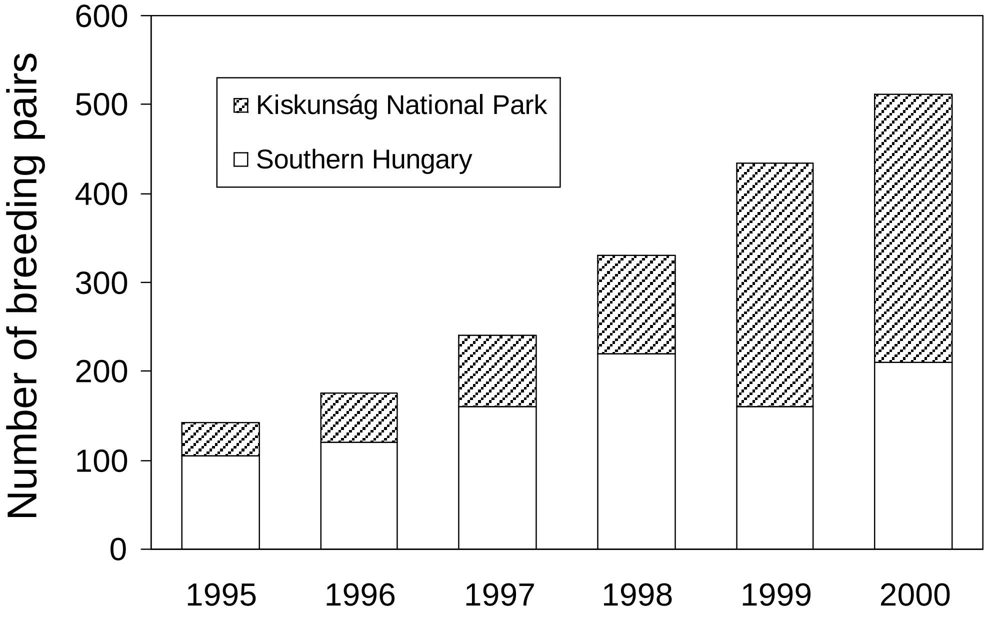

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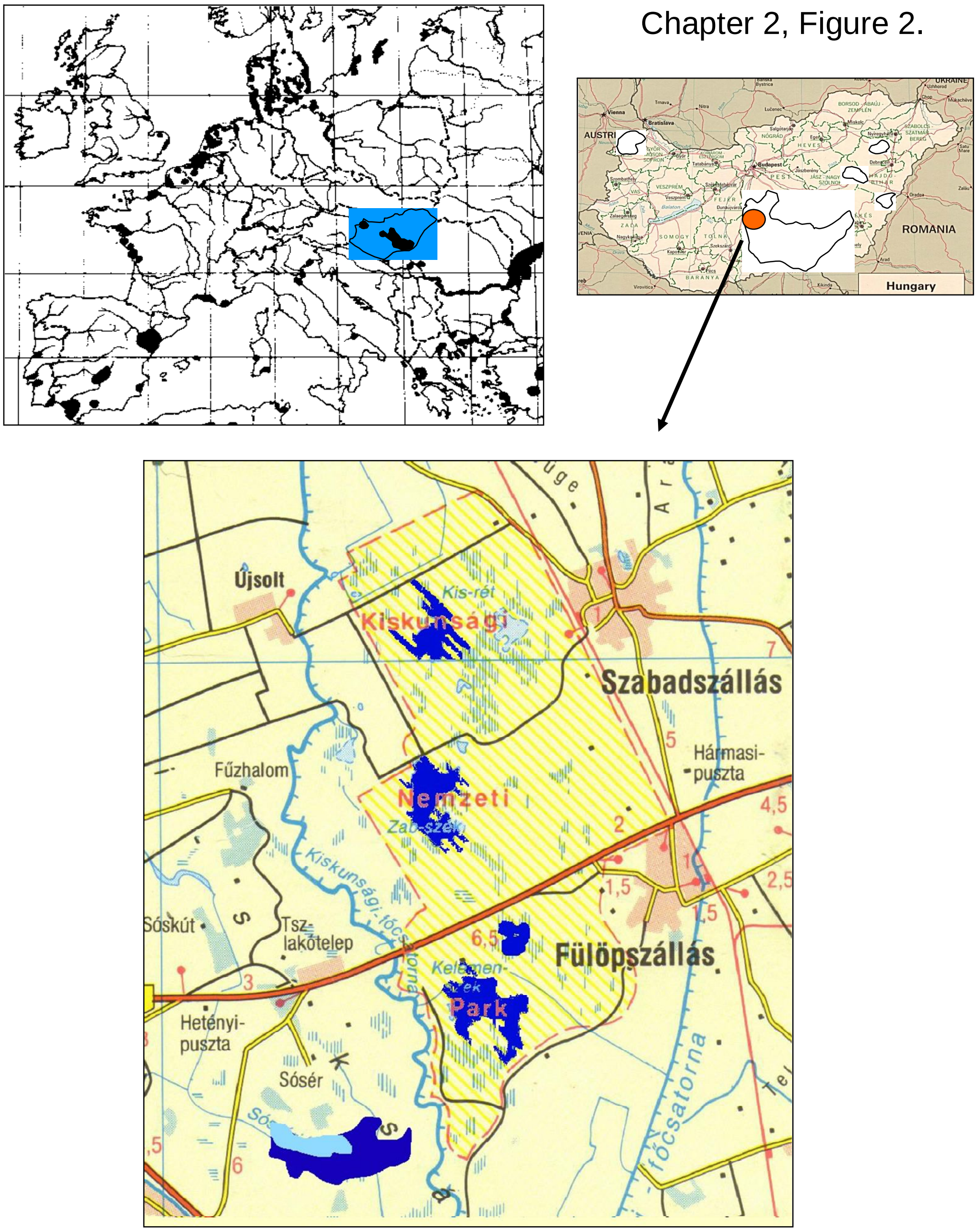

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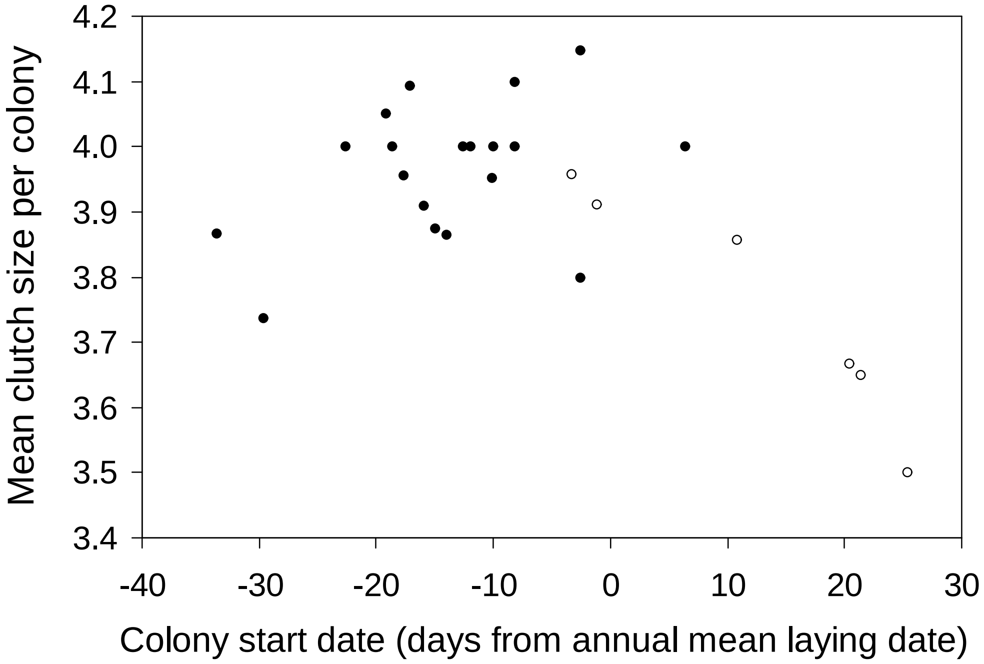

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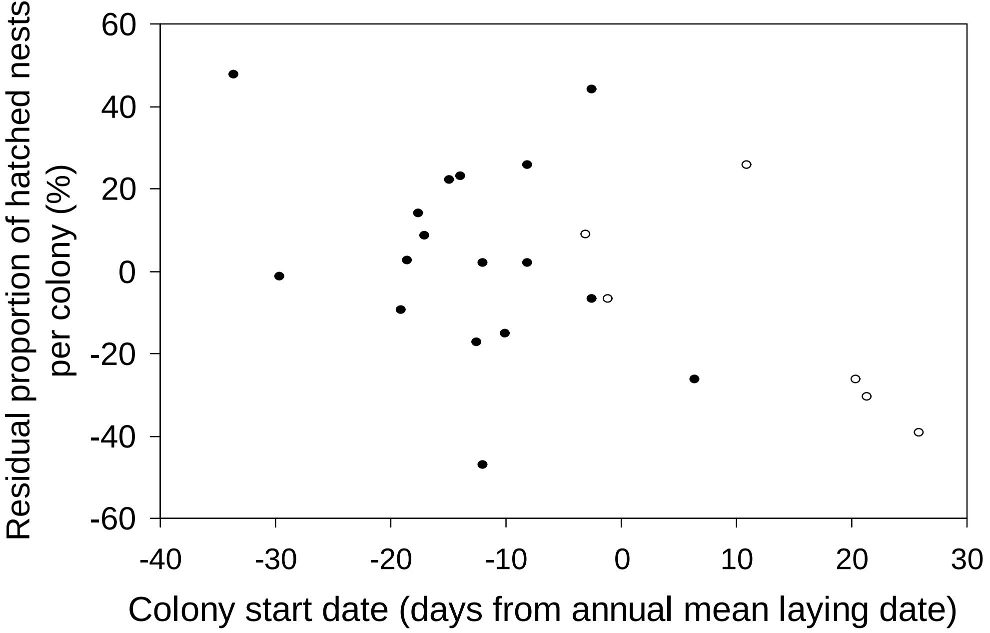

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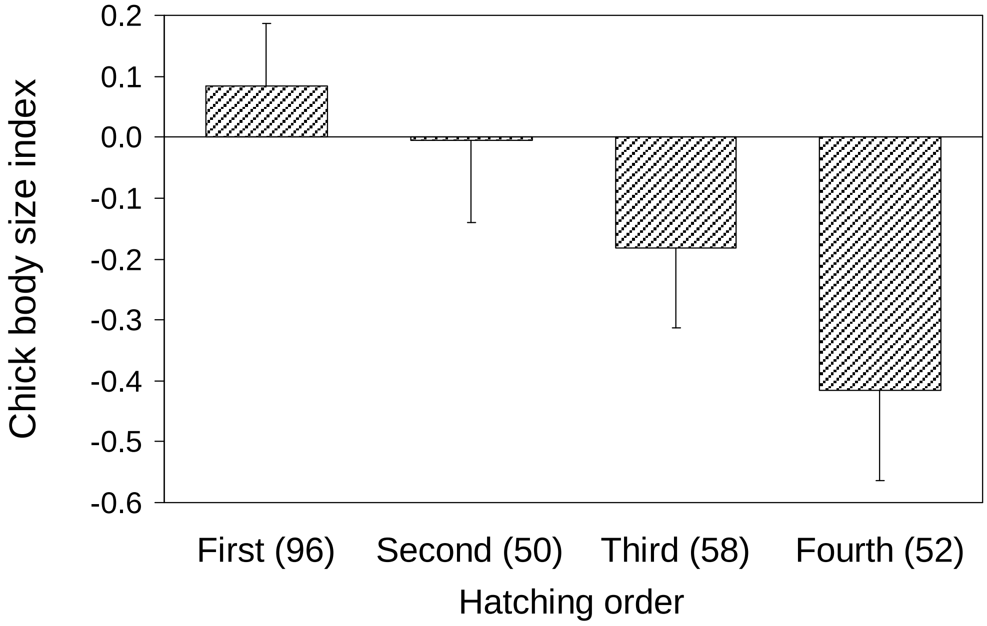

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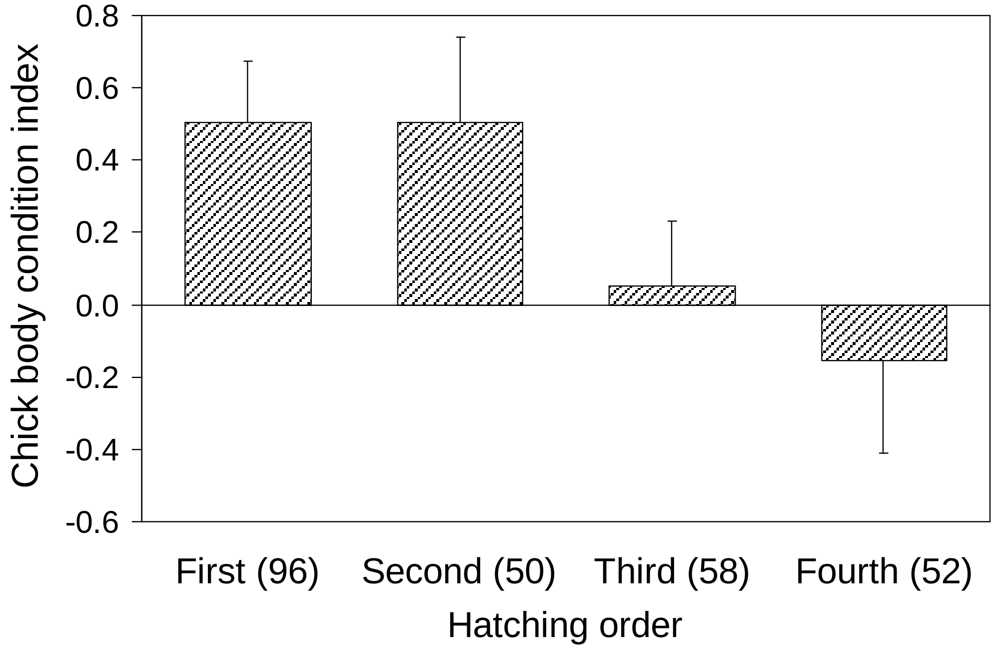

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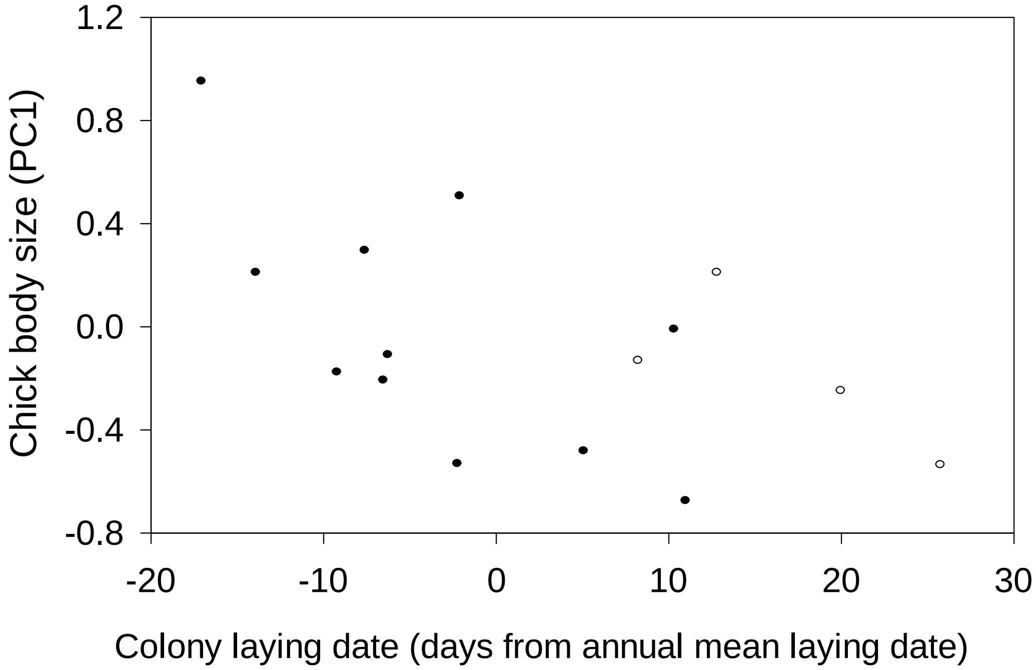

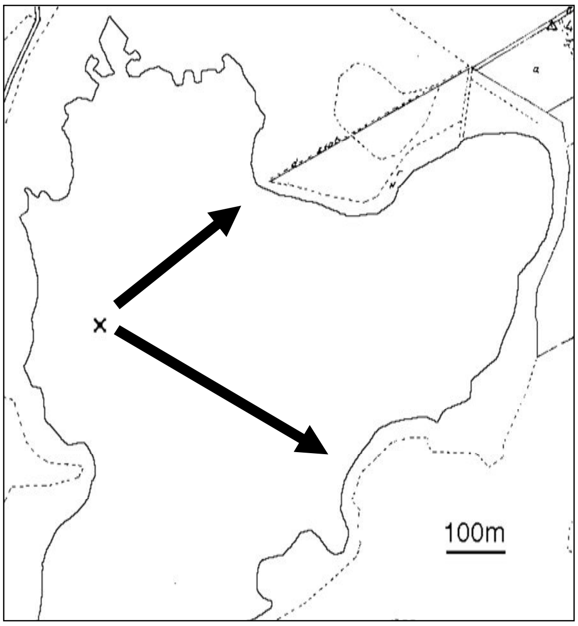

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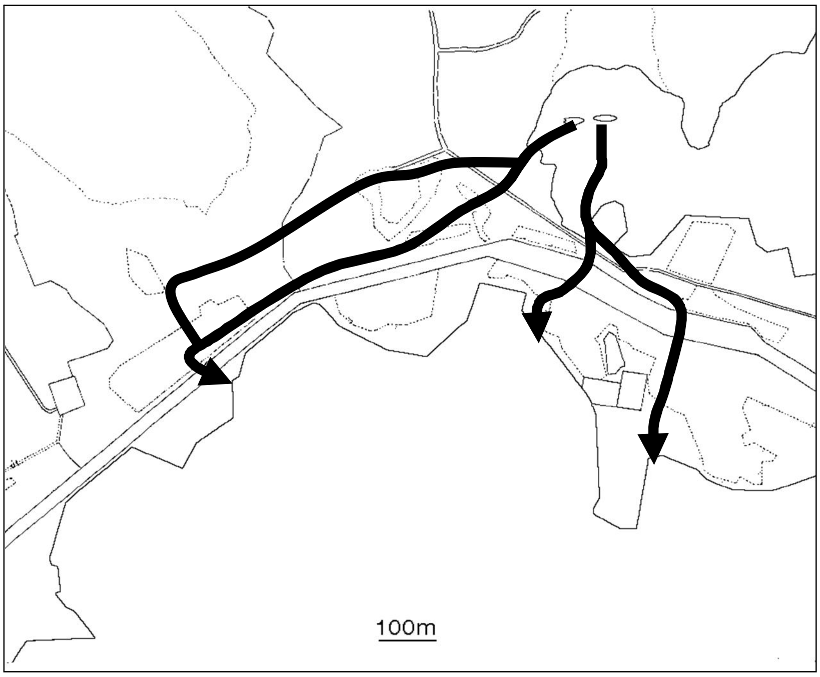

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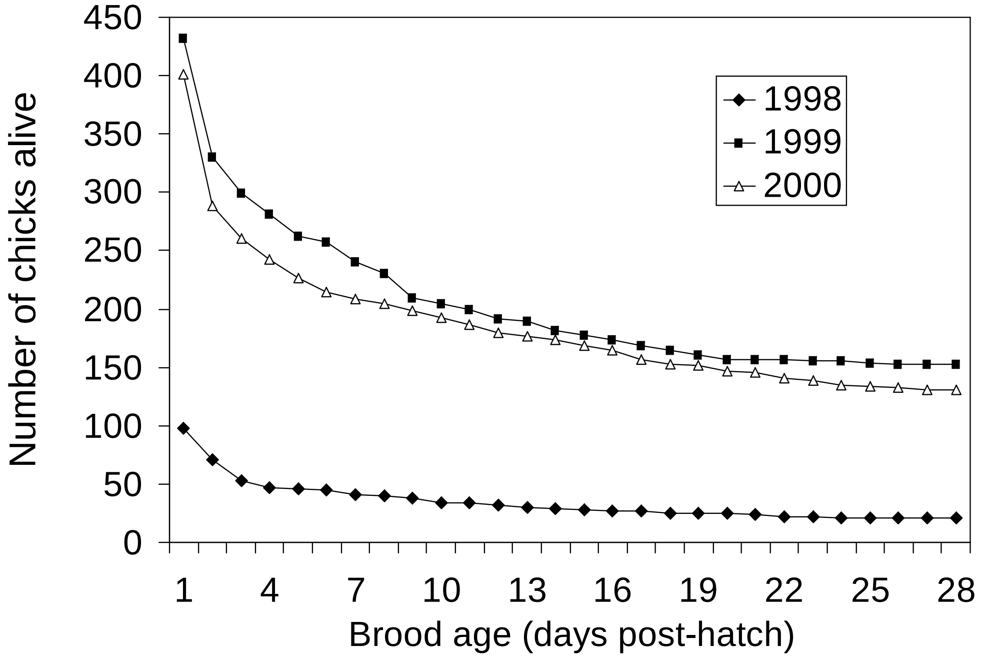

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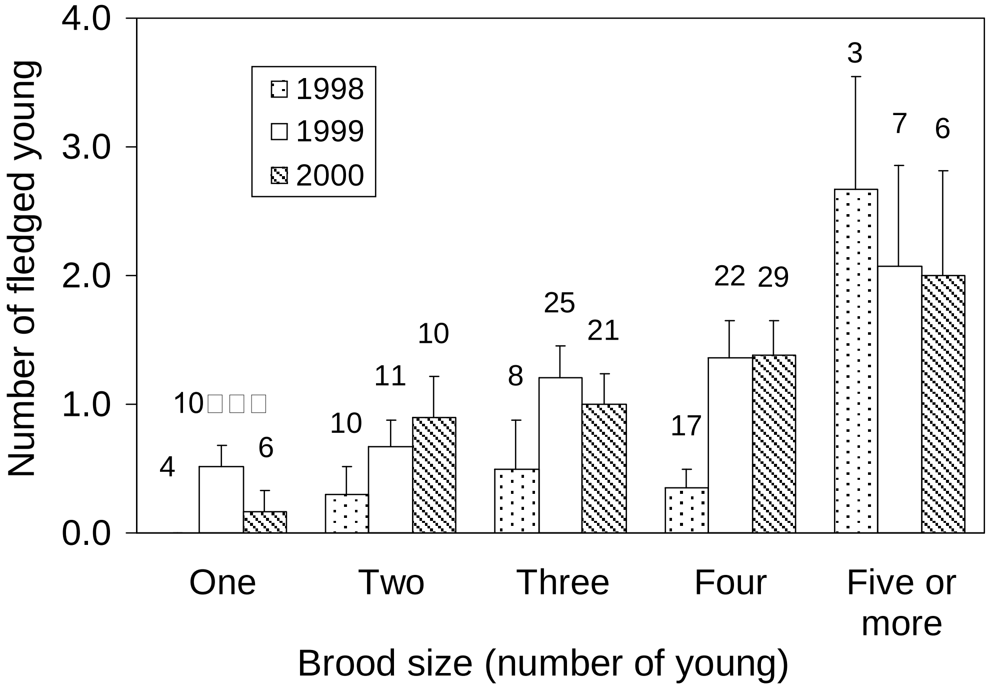


CHAPTER 3. ADOPTION IN AVOCETS: NATURAL HISTORY AND TESTS OF PROXIMATE HYPOTHESES

3.1. INTRODUCTION

Alloparental care, when young are cared for by adults other than their genetic parents (Riedman 1982; Skutch 1987), has been reported in over 220 bird species (Brown 1987). The most widespread form of alloparental care is adoption or brood amalgamation, when adults, besides caring for their genetic young, provide parental care to non-filial young that become members of their family group after hatching.

The proximate hypotheses proposed for the evolution of adoption can be distinguished by whether they imply benefits for the adopted chick, the adopting adult or both (**Table 1.**). Although adoption can be found in species with altricial young, 'true' adoptions are more likely in precocial birds (Pierotti 1988). The various costs and benefits of adoption have been studied in several species of waterfowl (ducks and geese of the order *Anseriformes*), and gulls and terns (order *Charadriiformes*, family *Laridae*).

In waterfowl adoption often has been interpreted as beneficial for both the adopted chicks and the adopting adults because chicks in larger broods survive better either through the increased dominance of larger broods over smaller broods (Lazarus & Inglis 1978; Schindler & Lamprecht 1987; Black & Owen 1989a; Williams 1994; Loonen et al. 1999) or through a dilution of predation (Munro & Bedard 1977a; Kehoe 1989; Nastase & Sherry 1997). Numerous studies, however, have found no evidence for costs or benefits of adoption and supported the view that adoption is neutral (Williams 1974; Titman & Lowther 1975; Patterson et al. 1982; Warhurst & Bookhout 1983; Bustnes & Erikstad 1991; Gosser & Conover 2000). Still other studies found behavioral costs (e.g. increased vigilance by parents with larger broods; Forslund 1993; Sedinger & Raveling 1990).

Adoption in gulls and terns appears to arise from a drive by young, small and disadvantaged chicks to gain adoption into broods where they gain advantage as the largest chicks (Graves & Whiten 1980; Pierotti & Murphy 1987; Roberts & Hatch 1994). Adoption incurs costs for the adopting adults because it reduces the number of their own young that can be reared to fledging (Carter & Spear 1986; Pierotti & Murphy 1987; Brown et al. 1995; Brown 1998). These countervailing interests create an intergenerational conflict (Pierotti & Murphy 1987), and, in most species, adoption is suggested to result from a reproductive error by the foster parents (Carter & Spear 1986; Knudsen & Evans 1986; Pierotti & Murphy 1987; Morris et al. 1991; Quinn et al. 1994; Roberts & Hatch 1994; Saino et al. 1994; Brown et al. 1995; Brown 1998; Oro & Genovart 1999).

In spite of extensive studies of adoption in waterfowl, and gulls and terns, the adoption behavior of precocial birds in other taxa remains virtually unknown. For example, numerous shorebirds (order *Charadriiformes*, families *Scolopacidae*, *Charadriidae*) have been reported to adopt foster chicks (Skutch 1976; Cooper & Miller 1992; Lanctot et al. 1995), however, adoption has never been explicitly studied in these large families.

The objective of this paper is to present data on, and test proximate hypotheses of, adoption in a colonially nesting shorebird, the Pied Avocet (*Recurvirostra avosetta*). The parental care system of avocets, and shorebirds in general, differs from that of waterfowl in that they have smaller clutch and brood sizes, and differs from that of gulls and terns in that shorebirds usually do not feed their young. The unique parental care system and life history of shorebirds makes it possible that selection acting on adoption may work differently in this group compared with the other two, well studied taxa. Based on previous hypotheses of adoption (reviewed in Chapter 1) and on the natural history of avocets I formulated proximate hypotheses that potentially explain adoption this species (Table 1.). Most hypotheses concentrate on only one mechanism of how adoption can be beneficial or costly, and they are not mutually exclusive. Using individual marking of chicks, I collected data on the occurrence, formation and frequency of adoptions and measured the potential costs or benefits of adoption for both the adopted chicks and the adopting adults, and used these data to test the predictions of each proximate hypothesis described in Table 1.

3.2. METHODS

3.2.1. General field methods

3.2.1.1. Study sites and study period

Fieldwork was conducted in a population of avocets breeding on alkaline lakes in the Kiskunság National Park (KNP) in central Hungary, from 1998 to 2000. Alkaline lakes, varying in size from 2-3 ha to 500 ha, are natural habitats of avocets. Fieldwork was also conducted in artificial habitats (fishpond and reconstructed wetland) because of their importance in avocet nesting. Avocets do not use every site every year and fieldwork was concentrated in areas of high nesting density and good accessibility in each year. Data from six alkaline lakes and two artificial sites are included in this study. More details on habitat and study sites can be found in Chapter 2.

3.2.1.2. Model species

The Avocet is a middle-sized, pied-plumaged shorebird breeding mostly in coastal areas in Europe and near alkaline lakes to the east of the Black Sea. Its main breeding habitats are salt marshes, salt evaporating ponds on the coast and large alkaline or saline lakes inland (Cramp & Simmons

1983; Hagemeijer & Blair 1997). Avocets nest in colonies, which are often formed on small islands. The species is monogamous and both parents care for young. The chicks are fully precocial and are able to walk and feed on their own a few hours post-hatch. Details on the breeding biology of avocets are given in Chapter 2.

3.2.1.3. General fieldwork

Nests were located by searching areas used by avocets for nesting. Every nest was numbered, marked and recorded on a map. The length, breadth and mass of the eggs was measured and eggs were floated to determine incubation stage, from which the expected date of hatching was estimated (Chapter 2).

Colonies that contained hatching nests were searched for young chicks at least once per day and the chicks were considered to belong to the nest in which they were found. Chicks were measured (culmen length, tarsus length and body mass) and banded with a brood-specific combination of two plastic color-bands and a metal band above the tarso-metatarsus less than 24 hours after hatching. Hatching order, if known, was indicated by different colored tapes attached to the metal band of the chicks. Colony visits were limited to 1 hr in cold weather and 0.5 hr in warm weather. A more detailed description of field methods can be found in Chapter 2.

Broods were monitored by locating families during their movement from the colony and in the chick-rearing areas. Searches were conducted every two or three days using a telescope to find vigilant adults and identify their chicks. During observations, I used hunting blinds or a car as observation points positioned at large distances from families to minimize disturbance. The location of territories and composition of avocet broods were recorded on habitat vegetation maps. A chick was considered dead if it was not seen on at least three consecutive observation bouts. Fledging was defined as living to 35 days, the age when juveniles are able to fly.

3.2.1.4. Behavioral observations

Behavioral observations were conducted to estimate the time budgets of both adults and young in as many broods as was possible. Behavioral observations were made when a brood was first seen to occupy a territory in the chick-rearing areas. If more than one brood was available for behavioral observation on any given occasion, I randomly chose the order in which observations were made. Broods were observed only once per day for either adult or chick behavior with the latter enjoying a priority because chick behavior was more difficult to observe than adult behavior.

Behavioral observations lasted for 30 minutes per family group for both adults and young. Adult behavior was recorded continuously by measuring the time spent with each behavior using a stopwatch. Adult behavior types included self-maintenance behavior (feeding, preening, resting, walking) and parental behavior (brooding, calling to the chicks, defense against predators, leading, territorial aggression against conspecifics and non-predators, vigilance).

Chick behavior was recorded instantaneously for every chick once every minute for 30 minutes. Chick behavior included being brooded, crouching, feeding, preening, resting and vigilance. In every 5th minute, I also estimated the distance between the vigilant parent and every chick using the height of the vigilant parent (ca. 0.4 m) as a template.

3.2.1.5. Sampling of food availability

I quantified territory quality by measuring the abundance of potential food items (aquatic invertebrates: waterbugs *Heteroptera*: *Corixidae*, *Notonectidae* and *Gerridae*, dragonfly larvae *Odonata*: *Anisoptera* and *Zygoptera*, water beetle larvae *Coleoptera*: *Dytiscidae*, *Gyrinidae*, chironomid larvae *Chironomidae* and annelid worms *Oligochaeta*) on the territory of as many broods as was possible. Sampling the food base was conducted once in 1998 and twice in 1999 and in 2000. Territories were selected for sampling only if the chicks were young (< 2 wk old; mortality of chicks is highest during the first week after hatching) and if the brood was observed on the same territory at least twice in 4-5 days.

The sampling location was standardized in the center of each territory in water depths of 3-4 cm. I enclosed a known area of water using an open-ended plastic cylinder (diameter 0.45 m) open on both ends and collected all aquatic invertebrates from within the known volume of water using a sweepnet (mesh size 0.2 mm). Macroscopic (>0.5 mm) aquatic invertebrates were stored in jars, preserved in 70% ethanol, and identified in the laboratory. The abundance of invertebrates was calculated by dividing the total number of invertebrates collected in a sample by the volume of water from which it was collected.

3.2.2. Variables and statistical analyses

Egg volume (cm^3) was calculated and fresh egg mass (g) was estimated according to formulae by Hoyt (1979) and parameterized with coefficients derived from actual measurements of avocet eggs. The estimated values did not differ from measured values (paired t-test, $p > 0.3$).

To quantify adult quality, I used indirect measures that usually positively correlate with adult quality in shorebirds (laying date, clutch size, egg size, number of young hatched, territory quality, proportion of time spent with parental behavior). Direct measures of adult quality (e.g. body size) were not available because adults were not captured and measured in this study.

Chick body size variables were highly correlated, and were reduced to a single variable by a principal component analysis. Body condition of chicks at hatch was estimated by the residuals from a linear regression of body mass on tarsus length. This variable is important for precocial chicks because they rely on their yolk reserves for survival during the first days after hatch (Starck

1993). To avoid pseudoreplication, I averaged chick body sizes for broods and used broods as data points in most analyses. The difference between the brood average and the body size of individual chicks was used to quantify individual chick quality.

Pseudoreplication may be present in the data combined from three years if some pairs or adults nested in more than one year. However, this was unlikely because only one of the marked adults that bred in at least one of the study years (n = 25) was observed to breed in more than one year. However, I treated the years separately in relevant analyses.

Sample sizes differ among statistical tests because complete information was not available for every brood. Data from three years were pooled. However, I controlled for yearly variation where it was appropriate (Chapter 2). Parametric tests were used only if the data met the assumptions of such tests. Homoscedasticity was tested by F_{max} and Bartlett-tests and residual plots, and normality was checked using the Kolmogorov-Smirnov test (Zar 1984). If the data did not meet the requirements of parametric tests even after transformations I used non-parametric tests. Means and ± 1 S.D.s are reported in the text and means ± 1 S.E.s are shown on graphs. I used two-tailed probabilities and $\alpha = 0.05$ in statistical tests.

3.3. RESULTS AND INTERPRETATION

3.3.1. The natural history of adoption in avocets

3.3.1.1. The frequency of adoption

I observed adoption in 53 broods (21.7% of broods resighted at least once, n = 244 broods). These events involved 92 adopted chicks (13.2% of the chicks resighted at least once, n = 697 chicks). The proportion of adopting broods was 16% in 1998 (n = 25 resighted broods), 20.7% in 1999 (n = 116) and 24.3% in 2000 (n = 103) (G = 0.974, df = 2, p = 0.6144). The proportion of adopted chicks was 9.9% in 1998 (n = 71 resighted chicks), 10.9% in 1999 (n = 331) and 16.6% in 2000 (n = 295) (G = 5.504, df = 2, p = 0.0638).

The average number of chicks adopted into a brood was 1.7 ± 1.16 (range 1-6). Adopting pairs (n = 53) had on average 3.1 ± 1.05 (range: 1-5) chicks before adoption and 4.8 ± 1.43 (range: 3-9) chicks after adoption. Four pairs (7.5%) had one chick of their own before adoption, whereas 12 pairs (22.6%) had two chicks, 25 pairs (47.2%) had three chicks, 11 pairs (20.8%) had four and one pair (1.9%) had five chicks before adoption. Most pairs adopted one chick (30 broods, 56.6% of adopting broods), whereas 15 pairs (28.3%) adopted two chicks, four pairs (7.5%) adopted three chicks, and two pairs (3.8%) adopted four and six chicks, respectively (Figure 1.).

When two chicks were adopted (n = 15 cases), they usually belonged to different broods (n = 11 cases), whereas in four cases they were from the same brood. When three chicks were adopted (n = 4 cases), the adopted chicks had come from two different broods in three cases, whereas in one case all three adopted chicks were from the same brood. When more than three chicks were adopted (n = 4 events), the adopted chicks came from three different broods.

In most cases, the adopted chicks separated from their natal brood and gained adoption elsewhere while their siblings were alive and being cared for by their own parents (71 adopted chicks, 87.7% of 82 cases in which the fate of the deserted brood could be determined). However, in 10 cases (12.3%), the natal brood ceased to exist as a functional unit either because the other chicks died (n = 3 cases), or were abandoned by their parents or because the parents were lost due to predation (n = 7 cases). I could not differentiate between the latter two causes because adults were not marked.

3.3.1.2. The occurrence of adoption in space and time

Adoptions occurred throughout the brood-rearing period, but were more frequent during early brood-rearing. Thirty-two adoptions (60.4%, n = 53 events) occurred before or during the departure of broods from the island nesting colonies. Six adoptions (11.3%) took place during brood movements. In 12 cases (22.6%) adoption occurred most likely in the colony but its exact location and time could not be confirmed, only that it had taken place before the broods reached the feeding areas. Three adoptions (5.7%) occurred in the brood-rearing areas.

Fifty-nine chicks (64.1% of adopted chicks, n = 92) were adopted in the nesting colony, whereas 10 chicks (10.9%) were adopted during brood movements (Table 2.). The adoption of 20 chicks (21.7%) occurred most likely in the colony, but it may have also taken place during brood movement. Finally, adoptions in the feeding areas involved the transfer of three chicks (3.3%).

3.3.1.2.1. Adoption in the nesting colony

The asynchronous hatching of eggs within a nest played an important role in the formation of adoptions in nesting colonies. In 64% of the nests monitored (n = 364 nests) the hatching of eggs lasted for two or more days (**Chapter 2**). During this period one parent led the older chicks to the closest water on the edge of the island colony. The parent defended a small territory on the shoreline, and chicks fed on their own within the territory. The other parent usually incubated the eggs or younger chicks in the nest. When several broods were hatching at the same time, chicks sometimes intermingled on the shoreline because parents were busy defending their territory from other adults and did not behave aggressively towards alien chicks.

Adoptions typically formed when broods left the nesting colony. When parents called and led their chicks away, sometimes chicks from other broods also joined the departing brood. I witnessed two such cases in an island colony in 1999. In other cases some of the departing pair's own chicks remained on the island and became adopted by another brood. I did not directly observe such cases, however, they could be inferred from later resighting observations.

In some cases, parents left the nesting island before the last-hatching chick joined the brood. These chicks attempted to gain adoption into one of the neighboring nests. The incubating adults initially pecked at alien chicks, but later accepted them. I observed abandoned chicks gaining adoption into nests that were only about halfway through incubation (n = 1 nest) and into nests that were less than two days before hatching (n = 3). I never observed parents abandoning their nest after adoption. In at least three cases, the chick gained only temporary entry into nests with eggs, and was eventually accepted by adults with chicks. Chicks gaining adoption into nests sometimes died in, or near, the nest (n = 6 cases). I did not observe strong adult aggression toward chicks or injuries on the dead chicks, therefore, it is likely that they starved to death.

The motivation of chicks to leave the natal brood while the brood was still in the colony is not clear (Table 2.). Twenty-two chicks (37.3% of the chicks adopted in the colony, n = 59) were the oldest (first-hatched) chicks in their natal brood and 14 (23.7%) chicks were second- or third-hatched chicks. These chicks likely left their incubating parents to feed with other chicks and left the nesting island in the foster brood earlier than their natal brood was ready to leave. In contrast, fourteen chicks (23.7%) were the last chicks to hatch and were abandoned by their parents. These chicks became adopted in other broods and left the nesting island later than did their natal brood. Three chicks (5.1%) became adopted after their siblings died from attacks by gulls and terns. Finally, in 10.2% of the cases none of the above conditions could be confirmed. Chicks that left their natal brood on their own are defined here as ‘unforced’ adoptees, whereas chicks that gained adoption after the loss, or the early departure, of their natal brood are called ‘forced adoptees’. Pairs whose chick(s) became unforced adoptees are termed ‘donors’. Some pairs (n = 11) were both adopters and donors; these pairs were excluded from analyses where it was appropriate.

3.3.1.2.2. Adoption during brood movements and in brood-rearing areas

Ten chicks (10.9% of the adopted chicks, n = 92) were adopted during brood movements in six adoption events. When pairs moved their broods from the nesting colony to feeding sites, adults usually showed territorial behavior and aggression toward other adults. During territorial fights the chicks intermingled, and it was possible for them to end up in an alien brood. Although none of the brood encounters that I observed resulted in permanent adoption, such a scenario could be inferred from resightings in six cases.

Finally, resighting observations suggested that three adoptions occurred after the pair and their broods completed movements and settled in the brood-rearing areas. Here pairs defended territories from other adults and also chicks, but in several cases chicks were seen wandering from one territory into another without being chased back by the owner of the territory. In such cases, the chicks could remain in the territory of the alien brood and could become adopted there.

3.3.1.2.3. Brood amalgamation

I observed brood amalgamation in two cases, when chicks from several broods merged, and were cared for by several adults. Both cases appeared to result from unusual circumstances. In the first case, the predation of hatching nests in a colony by a badger (*Meles meles*) presumably caused some adult avocets to leave their young. Five chicks from three broods formed the core of the amalgamated brood, which was attended by three to five adults. Six chicks from three other broods also joined the amalgamated brood temporarily several times during the fledging season.

In the second case, landscape morphology restricted brood movements to a narrow passage between lakebeds used by broods as feeding sites. Pairs and their broods crossing this area frequently became involved in territorial fights during which the chicks could mix freely among broods. Some adults apparently abandoned their young, leading to the formation of an amalgamated brood of 10 chicks from four broods, which was attended by four adults. These cases illustrate that brood amalgamation occurs in avocets; however, it appears to be rare.

3.3.2. The costs and benefits of adoption – tests of proximate hypotheses

3.3.2.1. Mutual benefit hypotheses

3.3.2.1.1. Antipredatory action hypothesis

This hypothesis (Table 1.) predicts that larger broods are better at detecting predators (Prediction 1) or at defending against predators than are smaller broods (Prediction 2).

During 26 hours of observations of chick behavior, I never observed chicks participating in either the vigilant behavior or the mobbing of predators by parents. Chicks spent most of their time feeding (48.5 ± 28.39%), being brooded (19.0 ± 27.55%), resting (14.8 ± 23.04%), and in locomotion (9.8 ± 12.55%), whereas preening (4.7 ± 7.41%) and crouching (1.2 ± 2.86%) were less common. Older chicks showed vigilant behavior (2.0 ± 4.49%), but even in such cases chicks never detected predators, and relied on their parents for warnings of predators. Chicks were never observed to participate in the defense of their brood and usually they ran for cover at the approach of predators. These observations suggest that chicks do not play a role in either the detection of, or the defense against, predators (Prediction 1 and 2 not supported).

3.3.2.1.2. Brood-dominance hypothesis

The brood-dominance hypothesis (Table 1.) predicts that adults with larger broods are dominant to adults with smaller broods (Prediction 1). Such dominance relationships may result in larger broods occupying territories better than those of smaller broods (Prediction 2).

Neither the duration, nor the proportion, of time parents spent with territorial aggression was related to brood size (duration: $F_{4,42} = 0.297$, $p = 0.8781$; proportion: $F_{4,55} = 0.254$, $p = 0.9058$, Prediction 1 not supported). During territorial interactions, parents generally chased intruding conspecifics and individuals of other species. The territory owners usually succeeded in chasing intruders away from their territory within a few minutes, and I have never observed a pair evict another brood from its territory. Shifts in boundaries of established territories took place only after several short periods of intense aggression occurring sporadically during a longer time period. Boundary shifts usually were small (only a few meters).

The abundance of potential food items (aquatic macroinvertebrate organisms) was positively correlated with the size of the brood occupying the territory when among-year differences in prey density (Kiss, B. & Lengyel, Sz., unpubl. data) were controlled for (Figure 2., Prediction 2 supported). This result indirectly suggests that larger broods may have been dominant over smaller broods during the establishment of territories, but that the behavioral observations that were conducted after broods settled into territories failed to detect this.

3.3.2.1.3. Dilution-effect hypothesis

The dilution-effect hypothesis (Table 1.) predicts that parents with smaller broods are more likely to adopt than are parents with larger broods (Prediction 1), or that parents losing chicks in the nesting colony should attempt to compensate for that loss by adopting alien chicks (Prediction 2). If predation is important in chick mortality, larger broods would be more likely to be successful in fledging chicks than would smaller broods (Prediction 3), and more chicks should fledge from larger broods than from smaller ones (Prediction 4). Finally, chicks should gain adoption into broods that are larger than their natal brood (Prediction 5), and adopted chicks should have a higher fledging success than that of their siblings remaining in the natal brood (Prediction 6).

Pairs with two or three chicks were more likely to adopt than were pairs with one chick or with four or more chicks (Table 3., Prediction 1 partially supported).

Pairs that lost chicks in the nesting colony (n = 60 pairs) were more likely to adopt than were pairs that did not lose chicks (n = 120), because 26.7% of pairs which had lost chicks adopted whereas only 11.7% of the pairs which had not lost chicks adopted (Table 4., Fisher's p = 0.0183, Prediction 2 supported). More than half (57.9%) of the pairs that left chicks behind as they moved from the island (n = 19) became adopters whereas only 11.8% of the parents that did not leave chicks behind adopted (n = 161) (Fisher's p < 0.0001, Prediction 2 supported). Pairs whose chick(s) died at, or near, the nest (n = 21 pairs) or departed with another brood earlier (n = 30) were not more likely to adopt than were pairs whose brood was not changed by the death (n = 159) or early departure (n = 150) of chicks (Fisher's p > 0.3450 in both comparisons). Even though some pairs lost chicks before adoption, they increased the size of their brood through adoption from 3.7 ± 0.63 chicks to 4.7 ± 1.45 chicks (Wilcoxon matched pairs test, $Z = 4.373$, $n = 44$ pairs adopting in the colony, $p < 0.0001$). Although the number of chicks hatched by adopters, non-adopters and donors did not differ, adopting pairs had larger broods after adoption and before leaving the colony than did non-adopting broods, and donor pairs had the fewest chicks after losing chicks to adoption and at the time that they departed the nesting area (Figure 3.).

Broods that had at least three chicks were more likely to fledge young than broods that had only one or two chicks (Table 5., Prediction 3 supported; see also Chapter 2). Furthermore, brood size positively influenced the number of chicks fledged per brood (Figure 4., Prediction 4 supported; see also Chapter 2).

Unforced adoptees appeared to choose broods larger than their natal brood; target broods had 2.7 ± 0.87 chicks, whereas the natal broods had 2.0 ± 0.88 chicks (adopted chicks were excluded from the calculation of brood sizes, paired $t_{48} = 4.069$, $p = 0.0002$, Prediction 5 supported).

The fledging success of unforced adoptees (28.3%, $n = 46$ chicks of known fate) did not differ from that of their siblings remaining in the natal brood (28.9%, $n = 76$) (Table 2., Fisher's exact $p > 0.9999$, Prediction 6 not supported). The fledging success of unforced adoptees that went to larger broods (24.1%, $n = 29$) was also not different from that of their siblings remaining in the natal brood (37.5%, $n = 32$) (Fisher's $p = 0.2843$, Prediction 6 not supported).

When all adopted chicks ($n = 90$ chicks of known fate) were included, chicks that went to broods containing four or more chicks had a higher fledging success (61.1%, $n = 18$) than did chicks that went to broods with three or fewer chicks (18%, $n = 72$, Fisher's $p = 0.0052$). However, only four (8%) of the unforced adoptees ($n = 50$) went to broods that had four or more chicks (Prediction 6 not supported).

3.3.2.1.4. Heat-conservation hypothesis

The heat-conservation hypothesis (Table 1.) predicts that chicks seeking adoption should choose broods larger than their own because thermoregulation is more efficient in a larger group (Prediction 1). An alternative prediction is that chicks are closer to each other in larger broods, which may enhance heat conservation among chicks (Prediction 2).

More than half (60.9%) of the unforced adoptees (n = 46) went to broods larger than their own brood, whereas 21.7% of these chicks went to broods of the same size and only 17.4% went to broods that were smaller than their own brood (G = 7.153, df = 2, p = 0.0280, Prediction 1 partially supported).

In observations of adult behavior (n = 76 half-hour observations) the average estimated distance among chicks did not correlate with the size of the brood (Spearman r = -0.001, n = 56, p = 0.7533, Prediction 2 not supported). The minimum and average distance between young chicks was 0.2 ± 0.21 m and 1.2 ± 1.33 m, and these distances are likely to be too high for heat conservation to be effective among chicks (Prediction 2 not supported).

3.3.2.2. Adult benefit hypotheses

3.3.2.2.1. Adult-parenting experience hypothesis

The adult-parenting hypothesis (Table 1.) predicts that inexperienced adults gain parenting experience through adoption. In avocets, adopters already have chicks on their own and I have never observed pairs without chicks adopt. Thus, any additional experience would be through an increase in brood size, rather than parenting *per se*.

3.3.2.2.2. Adult quality hypothesis

I predicted that if adult quality is related to which adults adopt (Table 1.), adopters would either lay their eggs earlier (Prediction 1), lay more eggs (Prediction 2), have larger eggs (Prediction 3), hatch more chicks (Prediction 4), occupy better territories (Prediction 5), spend more time with parental and territorial behavior (Prediction 6) or fledge more of their own chicks (Prediction 7) than would non-adopters. I compared these variables among adopting, non-adopting and donor pairs.

Pairs that would become adopters later (n = 41 pairs with known laying dates) laid their first egg 1.9 ± 5.47 days earlier than the mean laying date for all pairs, whereas pairs that did not adopt (n = 163) laid eggs 0.4 ± 6.87 days after the mean laying date, and donor parents (n = 36) laid eggs 2.6 ± 5.43 days before the mean laying date (Kruskal-Wallis test on residual laying dates that are independent from year and colony, H = 10.241, df = 2, p = 0.0060, Prediction 1 partially supported). Pairs that laid their eggs earlier than the mean laying date (n = 113) were more likely (26.5%) to become adopters than pairs that laid their eggs after the mean laying date (13.8%, n = 80) (Fisher's p = 0.0338, Prediction 1 supported).

Clutch size did not differ among pairs that later became adopters, non-adopters or donors ($F_{2,242}$ = 1.580, p = 0.2080, Prediction 2 not supported). There was also no difference among adopters, non-adopters and chick donors in either egg volume ($F_{2,158}$ = 0.523, p = 0.5939) or fresh egg mass ($F_{2,158}$ = 0.544, p = 0.5815, Prediction 3 not supported), when the among-year differences in egg size (Chapter 2) were controlled for by using the residuals of egg size.

Pairs that later adopted (n = 42) hatched 3.6 ± 0.62 young, whereas non-adopters (n = 167) hatched 3.3 ± 0.96, and donors (n = 36) hatched 3.6 ± 0.65 young (Kruskal-Wallis H = 4.651, df = 2, p = 0.0977, Prediction 4 not supported).

Prey density was significantly higher on territories of adopters than on non-adopters (Figure 5., Prediction 5 supported). Moreover, there was a positive correlation between the number of young fledged per brood and prey density ($r = 0.491$, $n = 63$, $p < 0.0001$).

There was no difference in the percentage of time spent in parental behavior among adopters (65.3 ± 31.40%, n = 20 pairs), non-adopters (69.2 ± 25.30%, n = 34) and donors (64.3 ± 39.25%, n = 6) ($F_{2,57} = 0.148$, $p = 0.8624$, Prediction 6 not supported). There also were no differences among adopting, non-adopting and donor pairs in the duration of territorial behavior (mean: 21.7 ± 16.30 s, $F = 0.520$, $df_{effect} = 2$, $df_{residual} = 44$, $p = 0.5982$) or the percentage of time spent with territorial behavior (mean: 3.3 ± 3.80%, $F = 0.945$, $df_{effect} = 2$, $df_{residual} = 57$, $p = 0.3949$, Prediction 6 not supported).

Adopters were more likely to fledge at least one of their own chicks than were non-adopters or donors, because 81.1% of the adopting pairs (n = 37) were successful, whereas only 44.0% of non-adopters (n = 166) and 47.1% of donors fledged young ($G = 17.929$, $df = 2$, $p = 0.0001$). Five of the adopting pairs fledged adopted chicks but none of their own young; these pairs were excluded from all analyses of fledging success.

Adopters fledged significantly more of their own young (1.5 ± 1.02 chicks, n = 37 broods) than either non-adopters (0.8 ± 1.08, n = 166) or donors did (0.7 ± 0.90, n = 34) ($F = 6.845$, $df_{effect} = 2$, $df_{residual} = 234$, $p = 0.0013$, Tukey-Kramer $q > 0.309$, $q_{critical}= 0.309$, $p < 0.05$, Prediction 7 supported). This difference was significant and in the same direction in the high predation year of 1998 ($F = 7.338$, $df_{residual} = 39$, $p = 0.0020$) and in the low predation years of 1999 and 2000 combined ($F = 3.551$, $df_{residual} = 192$, $p = 0.0306$). When brood size was included in the model as a factor, both adoption status and brood size were significant, while their interaction was not (Figure 6.). These results indicate that adopters are likely to benefit from increased brood sizes by fledging more of their own young (Prediction 7 supported).

3.3.2.2.3. Diluting-of-predation-risk hypothesis

The diluting-of-predation-risk hypothesis (Table 1.) makes the same predictions for adults as does the Dilution-effect hypothesis (Predictions 1 to 4). The two hypotheses differ in only one prediction for chicks. Chicks should not gain advantages or incur costs through adoption, i.e., adopted chicks should have a fledging success similar to that of their siblings remaining in the natal brood (Prediction 5).

The fledging success of unforced adoptees (Table 2., 28.3%, n = 46 chicks) did not differ from that of their siblings remaining in the natal brood (28.9%, n = 76, Fisher's exact $p > 0.9999$, Prediction 5 supported; see also Prediction 6 of the Dilution-effect hypothesis).

3.3.2.2.4. Exploitation-of-adopted-chicks-during-brooding hypothesis

The exploitation-of-adopted-chicks-during-brooding hypothesis (Table 1.) predicts that adopted chicks are exploited by the brooding parent by using them to thermally insulate its own chicks during brooding. Adopted chicks should be found farther from the vigilant parent than are resident chicks (Prediction 1), and they should be the last to be brooded by the parent (Prediction 2).

In behavioral observations in which brooding was observed (n = 10 observations), there was no difference in distance from the vigilant parent between adopted (1.3 ± 0.45 m) and resident chicks (1.3 ± 0.63 m) (paired $t = 0.050$, $p = 0.9613$, Prediction 1 not supported).

Resident and adopted chicks were equally likely to be the last to be brooded (Table 6., Prediction 2 not supported).

3.3.2.2.5. Selfish-herd hypothesis

The selfish-herd hypothesis (Table 1.) predicts that adopted chicks are more vulnerable to predation because they are often farther from the vigilant parent (Prediction 1) or are more frequently on the periphery of the brood (Prediction 2) than are resident chicks. Thus, adopted chicks may have a lower fledging success than that of the resident chicks (Prediction 3).

The average distance from the vigilant parent was 1.8 ± 1.18 m for adopted chicks and 2.0 ± 1.76 m for resident chicks (paired t = 0.933, n = 17 broods, p = 0.3649, Prediction 1 not supported). There was also no difference between the adopted and resident chicks when distance data from every 5th minute in the 30-min observations were analyzed as a repeated measures ANOVA ($F_{1,18} = 0.219$, p = 0.6457, Prediction 1 not supported).

The adopted chick was farthest from the vigilant parent in 39.1% of the cases when one chick was farther from the vigilant parent than all other chicks (n = 279 cases). This frequency did not differ from the frequency expected by assuming an equal probability of chicks on the periphery (35.5%, n = 27 adopted and n = 49 resident chicks, Yates corrected $\chi^2 = 0.190$, df = 1, p = 0.6628, Prediction 2 not supported).

The fledging success of adopted chicks (n = 92) was 31.5%, which did not differ from that of the resident chicks (36.8%, n = 152, Fisher’s exact p = 0.4098, Prediction 3 not supported).

3.3.2.3. Chick benefit hypotheses

3.3.2.3.1. Access-to-resources hypothesis

The access-to-resources hypothesis (Table 1.) predicts that chicks seek adoptions in order to gain access to resources that they would not gain access to in their own brood (Prediction 1). Because chicks should be able to evaluate the resources available in their natal brood and the target brood, most adoptions should occur after the broods arrive at the feeding territories (Prediction 2).

Prey density was higher on territories of adopters than on territories of non-adopters (Figure 5., Prediction 1 supported). However, only three of 53 adoption events (6%) occurred in the brood-rearing areas, where chicks could assess the quality of resources available for them in their natal brood and in the target brood, and 94% of the adoption events occurred before the broods reached the brood-rearing area (Fisher's exact $p < 0.0001$, Prediction 2 not supported).

It is possible that territory quality plays a role in adoptions at the time of hatching when the broods occupy small, temporary territories at the nesting sites at the edge of the water. However, preliminary results of the spatial variation of aquatic invertebrate abundance (Kiss, B. & Lengyel, Sz. unpubl. data) suggested that variation at the scale of temporary territories (few m) was unlikely to be high enough to explain the choice of territories rather than broods by chicks. Nevertheless, the territorial fights between adults could provide some clues of the quality (e.g. dominance status) of adults to chicks.

3.3.2.3.2. Chick-salvage-strategy hypothesis

The salvage-strategy hypothesis (Table 1.) predicts that chicks that are left for themselves after the departure or death of their siblings should attempt to join a brood, if they are to survive (Prediction

1). A slightly different prediction is that chicks seeking adoptions in alien broods after being left behind should survive better than do chicks not seeking adoptions (Prediction 2).

Limited observations suggested that all chicks whose siblings died near the nest, or that were left behind by their natal brood, made efforts to gain adoption into another nest or brood (i.e., I did not observe chicks that did not try to join another brood or nest). Young chicks are unlikely to survive without parental care because they need brooding at night and during cold weather, warnings from adults at the approach of predators, and a feeding territory defended by adults. Indeed, in 1961 sightings of chicks in my study, I have never seen unfledged chicks without one or more adults. These observations suggest that chicks that were abandoned by their natal brood gained adoption into another brood, or that chicks that did not join other broods died (Prediction 1 supported).

Chicks that were left behind by their parents (n = 21 chicks, Table 2.) salvaged their chances of survival by being adopted. Eight of these chicks (38.1%) fledged, and their fledging success was not significantly different from that of their siblings departing earlier with the natal brood (44.4%, n = 36, Fisher's p = 0.7824). However, the 38.1% fledging success was certainly higher than what could be expected for chicks that do not seek adoptions (0%, Prediction 2 supported). None of the three chicks that gained adoption in the nesting colony after their siblings died survived to fledging (Table 2.).

In summary, the fledging success of chicks forced to seek adoptions (33.3%, n = 24, Table 2.) was not different from the fledging success of their siblings that departed with the natal brood (38.1%, n = 42, Fisher's p > 0.9999), and was higher than could be expected for chicks not seeking adoptions (Prediction 2 supported).

3.3.2.3.3. Heat-gain-during-brooding hypothesis

Adopted chicks may have thermoregulatory benefits, if they position themselves in the center of the brood when parents brood the chicks. They may achieve this by becoming the first chick to be brooded by the parent (Prediction 1), therefore, they should position themselves closer to the vigilant parent than do resident chicks in situations when brooding occurs (Prediction 2).

Brooding of both the resident and adopted chicks occurred in 10 of 52 thirty-minute observations of chick behavior. There was no tendency for either the resident or adopted chicks to be the first or the last to be brooded during these brooding events (Table 6., Prediction 1 not supported).

In behavioral observations in which brooding was observed there was no difference in distance from the vigilant parent between adopted (1.3 ± 0.45 m) and resident chicks (1.3 ± 0.63 m) (paired t = 0.050, df = 9, p = 0.9613, Prediction 2 not supported).

3.3.2.3.4. The intergenerational-conflict hypothesis

The intergenerational-conflict hypothesis (Table 1.) predicts that chicks seeking adoptions are disadvantaged in their own brood (Prediction 1) and that these chicks attempt to gain adoptions into broods in which they are larger than the resident chicks (Prediction 2). The adopted chicks should increase their chances of survival compared to their survival probability in the natal brood (Prediction 3). To test these predictions, I used data on body sizes of chicks that were measured before they were one day old.

Hatching order influenced the body size of chicks, and first-hatched chicks were significantly larger than fourth-hatched chicks (Figure 7.). The effect of hatching order on chick body condition was not significant ($F_{3,252} = 2.496$, $p = 0.0604$). Hatching order, however, did not influence which chicks were adopted; the proportion of adopted chicks was 9.0% for first-hatched chicks (n = 144), 5.1% for second-hatched chicks (n = 78), 11.2% for third-hatched chicks (n = 107) and 7.2% for fourth-hatched chicks (n = 125) (G = 2.569, df = 3, p = 0.4630, Prediction 1 not supported). Furthermore, two-thirds (67.9%) of the chicks that were adopted in the nesting colony under known conditions (n = 53) were first to third-hatched chicks (unforced adoptees), which were unlikely to be disadvantaged in their natal brood (Prediction 1 not supported). In addition, fourth-hatched ('disadvantaged') chicks that were left behind by their parents were forced to initiate adoption and did not have the option of remaining in the natal brood.

The body size and body condition of unforced adoptees did not differ from those of their siblings remaining in the natal brood (Table 7., Prediction 1 not supported). There was also no difference in body size or body condition between adopted chicks and resident chicks (Table 7.), indicating that chicks seeking adoptions did not gain adoption into broods where they were larger than the resident chicks (Prediction 2 not supported).

Unforced adoptees (n = 46 chicks adopted in the colony) had a fledging success of 28.3%, whereas their siblings remaining in the natal brood (n = 76) had a fledging success of 28.9% (Table 2., Fisher's exact probability > 0.9999, Prediction 3 not supported; see also Prediction 6 of the Dilution-effect hypothesis).

3.3.2.4. Non-adaptive hypotheses

3.3.2.4.1. Accidental mixing hypothesis

The accidental-mixing hypothesis (Table 1.) predicts that adoption is a random, non-adaptive side-effect of high nesting density (Prediction 1), and/or the high synchrony within colonies (Prediction 2). Adoption also may result from a mixing of chicks during territorial aggression between the parents of two or more broods (Prediction 3). Adoption should not cause a change in either the breeding success of adults (Prediction 4) or the fledging success of chicks (Prediction 5).

All pairs that adopted chicks (n = 53) had nested in island colonies in which at least 10 nests hatched (n = 12) and adoptions were observed in each of these colonies. The only exception was the last colony in 2000, in which 15 broods hatched highly asynchronously. The number of adoption events was positively correlated with the size of the colonies (Spearman r = 0.847, n = 14 colonies with more than three broods, p = 0.0023, Prediction 1 supported). However, there was no correlation betweeen the proportion of adopting pairs and synchrony within a colony as measured by the standard deviation of julian hatching dates from the mean colony hatch date (Spearman r = -0.150, df = 14, p = 0.5879, Prediction 2 not supported).

Six adoptions (11.3% of n = 53 adoptions) occurred during brood movements, and these were likely to result from the mixing of chicks during territorial aggression by parents. Territorial interactions also were important in some adoptions in the nesting colony, because sometimes chicks from several broods intermingled on the shoreline while the parents were defending small territories from other adults. Furthermore, aggression between pairs influenced when broods departed from the island, which sometimes affected which chicks became part of which brood (Prediction 3 supported).

Adopting pairs fledged more young than did non-adopting adults (Figure 6., Prediction 4 not supported). The overall fledging success of adopted chicks (n = 90 chicks of known fate) was 32.2%, whereas the fledging success of their siblings remaining in the natal brood (n = 107) was 32.7% (Table 2.), which proportions were not statistically different (p > 0.9999, Prediction 5 supported).

3.3.2.4.2. Adult error hypothesis

The adult-error hypothesis (Table 1.) suggests that pairs adopt randomly wandering chicks because adults are incapable of recognizing and/or discriminating among chicks (Prediction 1). In addition, adoption should be costly to adults (Table 1.), and adopters should have a breeding success lower than that of non-adopters (Prediction 2).

I did not specifically test the chick recognition abilities of Pied Avocets. However, in the ecologically and behaviorally very similar American Avocet (*Recurvirostra americana*), parents start behaving aggressively towards alien chicks one week post-hatch (Lengyel et al. 1998). Several observations indicated that a delayed development of chick recognition also is possible in the Pied Avocet. First, I never observed adults behaving aggressively towards alien chicks (n = 50) in an experiment in which newly hatched chicks were transferred to their nest in 1999. Second, during observations of chick behavior, adults were seen to behave aggressively toward chicks only twice, at age 6 and 9 days post-hatch, respectively. In the first observation of aggression adults beat both their own chicks (n = 2) and the adopted chick sporadically for four minutes, whereas in the second observation only the adopted chick was beaten for less than 30 seconds. Chicks were not expelled by the adults in either of these cases. These observations suggest that avocets do not recognize their chicks, and/or do not discriminate between alien and their own chicks at an early age (Prediction 1 supported).

Adopters fledged more chicks than did non-adopters (Figure 6., Prediction 2 not supported; see also Prediction 5 of the Adult quality hypothesis).

3.3.2.4.3. Chick-error hypothesis

The chick-error hypothesis (Table 1.) predicts that chicks may end up in an alien brood because they are not able to follow their own parents (Prediction 1). Because adoption should be costly for the chicks that cease to be part of their natal brood (Table 1.), these chicks should have a fledging success lower than that of their siblings remaining in the natal brood (Prediction 3).

The information on how adoptions form, support the explanation that some chicks are not able to follow their parents (Prediction 1 supported). This may have been the case with some of the 21 chicks that were left behind at the nest by the natal brood (Table 2.). However, the exact cause of why these chicks were left behind could not be determined. Chicks that were left behind did not have a lower survival than did their siblings leaving with the natal brood (38.1% of them fledged, whereas 44.4% of their siblings [n = 36] fledged, Fisher's p = 0.7824, Prediction 3 not supported).

3.3.2.4.4. Maladaptation hypothesis

The maladaptation hypothesis (Table 1.) predicts that both the fledging success of adopted chicks, and the breeding success of adopting parents, should be lower than that of chicks staying in their own brood and than that of parents that do not adopt, respectively (Prediction 1). Two specific reasons for this may be that adults nest in such a density that has not existed previously and there has not been enough time for selection to act on the behavior (Prediction 2), or that broods that become larger by adoption are more easily detected by predators than are smaller broods (Prediction 3).

The overall fledging success of adopted chicks (n = 90 chicks of known fate) was 32.2% (Table 2.), whereas the fledging success of their siblings remaining in the natal brood (n = 107) was 32.7% (Fisher's p > 0.9999, Prediction 1 not supported; see also Prediction 5 of the Accidental-mixing hypothesis). Adopting pairs fledged significantly more of their own young than did non-adopters (Figure 6., Prediction 1 not supported; see also Prediction 5 of the Adult quality hypothesis).

It is unlikely that high breeding densities and adoption frequencies in avocets are novel phenomena in the last 100 years, because avocets had been known to nest in dense colonies in Hungary before 1890 (Chernel 1890) (Prediction 2 not supported) and elsewhere in Europe in the first half of the 20th century (Hagemeijer & Blair 1997).

Larger broods were more likely to be successful than smaller broods were (Table 5.), and brood size positively influenced the number of young fledged (Figure 4., Prediction 3 not supported; see also Prediction 4 of the Dilution-effect hypothesis).

3.4. DISCUSSION

Both the adopting adults and the chicks that are left behind by their parents appear to benefit from adoption. Adoption is frequent in the studied population; 21% of the pairs adopted chicks and 13% of the chicks were adopted. The frequency of adoption did not differ in the three years. There are no published data on the frequency of adoption in other populations of Pied Avocets, only that it does occur in other populations (Cadbury & Olney 1978; Cramp & Simmons 1983; H. Hötker, pers. comm.). In American Avocets, 20% of the pairs adopted chick in one year and 32% in another year (Lengyel et al. 1998). In Pied Avocets, most adoptions occur on, or near, the nesting island at, or around, the departure of broods to feeding areas. The synchronous hatching of nests within a colony and the asychronous hatching of eggs within a nest played a substantial role in the formation of adoptions. Both the synchrony of nests within a colony and asynchrony of eggs within a nest are general characteristics of avocets (Cadbury & Olney 1978; Cramp & Simmons 1983; Hötker & Segebade 2000; Chapter 2), therefore, it is unlikely that they were artifacts in this study. Two kinds of chick motivation could be distinguished. Unforced adoptees left their natal brood before their parents and siblings departed the nesting island. Forced adoptees were left behind by their parents and had to gain adoption if they were to survive. Adoptions also occur during movements of broods and in the feeding areas, where sometimes several broods amalgamate. However, adoptions outside the nesting colony are less frequent.

I found support for several hypotheses (see Table 1.). All predictions are supported only in the case of the Diluting-of-predation-risk and the Chick-salvage-strategy hypothesis. First, pairs that leave chicks behind at the nest are more likely to adopt than those that do not leave chicks at the nest. Second, even though some adopters lose chicks in the colony, on average they increase the size of their broods. Third, larger broods are more likely to fledge young than are smaller broods, and more young fledge from larger broods than from smaller ones. Fourth, even though the adopted chicks go to broods that are larger than their natal brood, their fledging success does not differ from that of their siblings remaining in the natal brood, which indicates that adopters but not the unforced adoptees benefit from adoption. Finally, chicks that are left behind by their parents salvage their survival chances by gaining adoption into other broods. However, the chick-salvage-strategy hypothesis applies only to forced adoptees and does not explain why the majority of the adopted chicks left their brood without being forced to do so.

I found partial support for four other hypotheses. The frequency of adoption increases with increasing colony size and the fledging success of adopted chicks does not differ from that of their siblings remaining in the natal brood (Accidental-mixing hypothesis). Larger broods hold territories of higher prey density than do smaller broods, which is consistent with the Brood-dominance hypothesis. Finally, chicks appear to choose broods larger than their own brood (Dilution-effect and Heat-conservation hypotheses).

Most of the supported predictions also are consistent with the explanation that adopters are higher-quality adults than are non-adopters (Adult quality hypothesis). First, pairs that adopt later in the season start laying eggs earlier than did non-adopters. The start of laying correlates well with dominance and adult quality in avocets because nest sites within a colony are decided during intense territorial fights among adults (Chapter 2). Pairs that establish a nest site and start laying eggs early are likely to be dominant over other pairs and the date of egg-laying is likely to be negatively correlated with adult quality in this species (Chapter 2). Second, adult quality also may explain why adopters occupy territories of higher prey density than do non-adopters or donors. This is possible, if adult quality or brood size and dominance in territorial interactions leading to the establishment of territories are positively correlated. For example, pairs with larger broods are dominant over pairs with smaller broods in several goose species (Boyd 1953; Hori 1964; Nastase & Sherry 1997; Lazarus & Inglis 1978; Loonen et al. 1999), and goslings in larger broods gain access to better resources than do goslings in smaller broods (Raveling 1970; Black & Owen 1989a; Kehoe 1989). My behavioral observations do not support this explanation because there are no differences in territorial behavior according to brood size or adoption status. However, my behavioral observations were conducted after broods settled in territories, and the dominance of adopters may have been important earlier. Finally, two observations suggest a non-random pattern in which of the pairs became adopters. First, adults with two or three chicks are more likely to adopt than pairs with one chick or pairs with four or more chicks. Second, pairs that lose chicks at the nest are more likely to adopt than pairs that do not lose chicks at the nest. These observations suggest that pairs with one chick may be lower-quality parents that can not compensate for their chicks lost at the nest. On the other hand, it is also possible that pairs with four or more chicks are better parents, which do not lose chicks at the nest and thus are not inclined to adopt chicks.

Adult quality also can play a role in the choice of broods by adopted chicks because unforced adoptees may choose foster broods based on the quality of the adults rather than on the number of chicks in their broods. Adults with broods in the colony spend much time with territorial interactions, which can provide clues about adult quality for chicks. For example, young of some duck species have been reported to group behind the most stimulating, “superbroody” females (Koskimies 1955; Ahlén & Andersson 1970; Kehoe 1989).

The benefits of larger broods to avocet parents were clearly demonstrated by this study. The most important source of chick mortality in this study was predation by aerial predators (harriers) and terrestrial predators (foxes and badgers) on young (< 1 week old) chicks (Chapter 2). If larger broods are not more likely to be preyed upon than are smaller broods, then the effect of predation can be diluted in larger broods. This may explain why larger broods were more likely to fledge young than were smaller broods and why the number of chicks surviving to fledging was higher in larger broods than in smaller broods. This difference was similar across years, but it was more pronounced in the high-predation year (1998) than in the low-predation years (1999 and 2000). Furthermore, both adoption status and brood size influenced the number of young fledged, and the lack of a significant interaction between these two factors indicates that the differences caused by adoption status were similar across the different levels of brood size. These results contradict those of Safriel (1975) who suggested that larger broods are more conspicuous to predators, and consequently are more likely to be preyed upon than are smaller broods. In Semipalmated Sandpipers (*Calidris pusilla*), chicks in larger than normal (five-chick) broods are less likely to survive to fledging than chicks in normal (four-chick) broods (Safriel 1975). Other studies of the relationship between brood size and chick survival have not reported such disadvantages of larger broods. Moreover, dilution of predation has been thought to be important in the amalgamation of broods in the Common Eider (*Somateria mollissima*) and in the White-winged Scoter (*Melanitta fusca deglandi*), because ducklings in larger broods have a survival advantage over ducklings in smaller broods (Munro & Bedard 1977a; Kehoe 1989).

It is not clear whether the relationship between adult quality and brood size is important in interactions among individuals in avocets. Brood size has been suggested to serve as an honest signal to indicate adult quality and dominance status in Barnacle Geese (*Branta leucopsis*) (Loonen et al. 1999). Because adults were not marked in my study, it was not possible to evaluate whether avocets use brood size as a signal of individual quality in mate choice during subsequent breeding attempts or in other interactions among individuals.

It is also not clear why some chicks left their own brood and gained adoption into foster broods, because they did not obtain survival benefits by doing so. The possibility of some gains, however, can not be excluded because it remains unknown what would have happened to chicks that “wanted” to be adopted but were prevented from doing so. The observations of how adoptions occur, and the fact that the fledging success of chicks did not change by adoption, suggest that two factors may be important in why chicks leave their own brood. First, unforced adoptees tended to be older, more mobile chicks than their younger siblings, and it is possible that their physiological demands (e.g. to feed) predisposed them to leave the natal brood. Second, leaving the natal brood may also arise from a non-adaptive drive of young chicks to join other chicks. These explanations seem plausible because at the time of leaving of the older chicks their younger siblings usually were still hatching or were in the nest under the incubating parent.

Forced adoptees clearly benefitted from adoption because they achieved the same survival as their siblings remaining in the natal brood. Furthermore, the fact that all chicks left behind by their parents tried to gain adoption provides two important insights into the chicks’ tactic in avocets. First, parental care is essential for chicks to survive. Second, chicks can and do actively pursue adoption, therefore, it is possible that unforced adoptees, beyond their pyhsiological demands or gregarious nature, also actively seek adoption into broods other than their own.

The adoptive behavior of avocets is peculiar in several aspects. First, it appears that there are no costs of adoption for either the parents or the adopted chicks. This agrees with previous suggestions that in fully precocial species, the costs of tolerating alien chicks in the brood are low or non-existent (Pierotti & Murphy 1987), because parental care is shareable or non-depreciable (benefits all young equally, Lazarus & Inglis 1986). Second, the alloparental care system of avocets potentially can be adaptive. Parents may obtain fitness advantages by adoption because the fledging success of their own chicks increases in larger broods. Chicks also may actively choose parents, however, their choice does not appear to be related to gains in fitness.

The alloparental care system of avocets shows similarities to those of rheas and geese. In the Greater Rhea (*Rhea americana*), adopters are likely to be superior parents because they spend more time vigilant, brood chicks more frequently and are more aggressive to conspecifics than are non-adopting parents (Codenotti & Alvarez 1998). Even though adopters are likely to be superior parents in avocets, behavioral correlates of adult quality could not be confirmed in my study. The benefits of larger broods in geese (*Anseriformes*: *Anatidae*) included higher dominance, access to better territories, and faster growth of chicks (Black & Owen 1989a; Loonen et al. 1999; Cooch et al. 1991). Even though my study could not discern all potential benefits of larger broods in avocets, it appears likely that the benefits of adoption in avocets are manifested by the advantages of larger broods.

Several ultimate-level hypotheses also may explain the adopting behavior of avocets. First, kin selection may operate, if the adopters and adoptees are relatives (Hamilton 1964; Riedman 1982). This explanation is possible in avocets, if the high synchrony of hatching within colonies is coupled with the nesting of related individuals in the same colony. Under such conditions, the inclusive fitness of the foster parent may increase above the fitness advantage obtained by adoption and may ultimately lead to an adaptive system of alloparental care. Second, reciprocal altruism (Trivers 1971) also has been proposed to explain adoption. However, this hypothesis assumes that adoption is costly for the adopter parents and beneficial for the donor parents. I did not find costs to adopters nor benefits to donors in avocets.

In conclusion, my results support the hypothesis that adoption provides fitness advantages to adults. Brood size increases by adoption, and pairs with larger broods occupy better territories and fledge more young than do pairs with smaller broods. However, an experimental manipulation is necessary to separate the effects of adult quality and brood size and evaluate the relative importance of these two factors in the alloparental care of avocets.

3.5. TABLES

Table 1. Proximate hypotheses of adoption tested in this study in the Pied Avocet (*Recurvirostra avosetta*). The fitness costs and benefits of alloparents is compared to the fitness of adults raising only their own genetic young, and the fitness of adopted chicks is compared to the fitness of chicks reared by their genetic parents. The currency of adoption for adults is annual breeding success, and for chicks it is fledging success.

Benefit	Hypothesis	Description	References
Mutual	Antipredatory action	Larger broods are better than smaller broods at detecting or defending themselves against predators.	1., 2.
benefit	Brood dominance	Pairs with larger broods are dominant over and occupy better territories than pairs with smaller	3., 4., 5.
	Dilution-effect	broods.	6., 3., 7., 8.
	Heat conservation	Predation risk per chick is smaller in larger broods.	2., 9., 10., 3.
		The heat loss of chicks is smaller in larger broods.	
Benefit	Adult parenting	Young and/or inexperienced breeders gain experience in raising chicks by adoption.	11., 12.
for the	experience		
adopting	Adult quality	Only adult of high quality adopt and brood size may serve as a signal for adult quality.	This study
adult	Diluting predation	Adults decrease the chance that their own chicks get depredated, while the survival of adopted chicks	1., 13., 5.
	risk	does not change.	
		Adopted chicks ‘insulate’ resident chicks by being on the periphery during brooding.	This study
	Exploitation during		
	brooding	Adults decrease the chance that their own chicks get preyed upon by exploiting the adopted chick.	3., this study
	Selfish herd		
Benefit	Access to resources	Adopted chicks access resources in the foster brood that they cannot gain access to in their natal	5.
for the	Chick salvage strategy	brood.	This study
adopted	Heat gain during	Chicks that are abandoned by their parents salvage their survival by adoption.	9., 14., 15., 16.
chick	brooding	The adopted chick has thermoregulatory benefits in the foster brood compared to its natal brood.	17.
	Intergenerational		18., 19.
	conflict	Disadvantaged chicks are selected to leave their natal brood and seek adoption by adults that are	
		unable to reject them.	
No	Accidental mixing	Adoption is a random process which does not influence the fitness of either participant.	20., 21., 22., 23.
benefits	Adult error	Adoption is a result of a lack or insufficiency of chick recognition by adults.	20., 22., 24.
	Chick error	Adoption results from a recognition error by chicks or their incapability to stay with the natal brood.	25., 26., 27.
	Maladaptation	Adoption is costly for both participants but has not existed long enough to be eliminated by selection.	25.

References: 1. – Kear 1970, 2 – Gorman & Milne 1972, 3. – Kehoe 1989, 4. – Pierotti 1991, 5. – Nastase & Sherry 1997, 6. – Black & Owen 1989a, 7. – Williams 1994, 8. – Loonen et al. 1999, 9. – Warhurst & Bookhout 1983, 10. – Carter & Hobson 1988, 11 – Riedman 1982, 12. – Schmutz et al. 1982, 13. – Larsson et al. 1995, 14. – Bustnes & Erikstad 1991, 15. – Roberts & Hatch 1994, 16. – Eadie & Lyon 1998, 17. – Birkhead & Nettleship 1984, 18. – Graves & Whiten 1980, 19. – Pierotti & Murphy 1987, 20. – Williams 1974, 21. – Patterson et al. 1982, 22. – Savard 1987, 23. – Savard et al. 1998, 24. – Titman & Lowther 1975, 25. – Holley 1984, 26. – Carter & Spear 1986, 27. – Saino et al. 1994

Table 2. Fate of chicks adopted in various locations and during the three years of the study. Unforced adoptees were those that had left their natal brood before the natal brood departed the nesting island, whereas forced adoptees were those that had been either left behind by their natal brood or whose siblings had died and were abandoned by their parents. Adoption events indicated as "In colony / during brood movement" most likely occurred in the nesting colony but the exact location could not be confirmed. In analyses of chick fledging success, these chicks (n = 20) were combined with chicks adopted in the nesting colony (n = 59).

Location of adoption event	**Motivation of adopted chick**		**Fledged**	**Died**	**Unknown**	**Total**
Nesting colony	Unforced	First-hatched	5	17	0	22
		Second or third-hatched	5	9	0	14
	Forced	Left behind	5	9	0	14
		Siblings died	0	3	0	3
	Unknown		0	5	1	6
In colony / during brood movement	Unforced	First-, second- or third-hatched	3	7	0	10
	Forced	Left behind	3	4	0	7
	Unknown		0	2	1	3
During brood movement	Unforced		0	2	0	2
	Forced	Siblings died	4	2	0	6
	Unknown		2	0	0	2
Feeding areas	Unforced		1	1	0	2
	Forced	Siblings died	1	0	0	1
		Totals	29	61	2	92

Table 3. The frequency of adoption in broods of different sizes. Parents with broods of two or three chicks were more likely to adopt than parents with one chick or parents with broods of four (n = 61 broods) or more chicks (n = 9) (G = 8.087, df = 3, p = 0.0443).

Number of resident chicks	One	Two	Three	Four or more	Total
Number of adopting broods	4	12	25	12	53
Number of non-adopting broods	24	30	47	58	159
Percentage of broods adopting	14.3	28.6	34.7	17.1	25.0
(Total)	(28)	(42)	(72)	(70)	(212)

Table 4. The number of adopting and non-adopting pairs losing chicks to different causes in the nesting colony. Pairs were defined as "Chicks lost to adoption" if their chicks became unforced (voluntary) adoptees. Pairs that lost chicks to more than one cause are listed in more than one cell of the table. One non-adopting pair lost chicks in each of the three ways listed, three non-adopting pairs lost chicks to both adoption and death, whereas 11 pairs (five adopters, six non-adopters) left chicks behind and also lost chicks to adoption. Pairs that both lost chicks to adoption and adopted chicks (n = 11 broods) were excluded from these analyses. Donors were pairs whose chick(s) were unforced adoptees elsewhere.

Chick loss	Cause of chick loss	Adopted	Did not adopt	Total
Lost chicks in colony	-	16	44	60
	Left chicks behind	11	8	19
	Chicks lost to adoption	5	25	30
	Death	5	16	21
Did not lose chicks in colony	-	14	106	120

Table 5. Number of successful broods (defined as producing at least one fledgling) as a function of brood size in. Data from the three years are combined, and broods that were used for experiments (n = 118) are excluded. The difference in proportions is significant (G = 15.493, df = 4, p = 0.0038).

	Number of chicks in brood				
Variable	**One**	**Two**	**Three**	**Four**	**Five or more**
Number of successful broods	5	10	31	38	12
Number of unsuccessful broods	15	21	23	30	4
Total	20	31	54	68	16

Table 6. The order in which chicks were brooded in half-hour observations of chick behavior. The first chick to be brooded was determined for all brooding events involving two or more chicks, whereas the last chick to be brooded was determined for cases when all chicks were brooded. Expected frequencies were calculated assuming an equal chance of chicks becoming first or last in the brooding order, weighed by the actual number of chicks (n = 17 adopted chicks, n = 49 resident chicks) monitored in behavioral observations in which brooding of both resident and adopted chicks occurred (n = 10 half-hr observations).

Brooding order	Observed frequency	Expected frequency	Fisher's exact p
Adopted first	9	6	0.5380
Resident first	16	19	
Adopted last	3	3	1.0000
Resident last	10	10	

Table 7. Comparison of body size, and body condition, of adopted chicks to their siblings remaining with the natal brood and to resident chicks in target broods. For the comparison of adopted chicks and siblings, only those chicks were included that gained adoptions without being forced to do so ('unforced' adoptees).

	Adopted chicks	Siblings of adopted chicks	Resident chicks in target broods	t*	df	p
Body size (PC1)	0.18 ± 0.850	-0.13 ± 0.842		1.757	42	0.0863
	0.27 ± 0.904		0.06 ± 0.710	0.988	39	0.3293
Body condition	0.68 ± 0.140	0.68 ± 0.050		1.138	45	0.2613
	0.68 ± 0.048		0.69 ± 0.048	1.474	39	0.1484

* Paired t-test

3.6. FIGURE LEGENDS AND FIGURES

Figure 1. The distribution of adoption events (n = 53) by the number of chicks in the brood of the adopting pair before adoption and the number of chicks adopted by the pair. Pied Avocet broods were monitored between 1998 and 2000 in the Kiskunság National Park in south-central Hungary.

Figure 2. The relationship between prey density on the territory and size of the brood occupying the territory. Prey density was quantified by the residuals of a one-way ANOVA in which year was the main effect and the log-transformed number of aquatic macroscopic invertebrates per liter water was the response variable. $r = 0.355$, $n = 63$, $p = 0.0040$.

Figure 3. Mean (± S.E.) brood size (number of chicks) of adopting, non-adopting and donor pairs at hatch (open bars) and after adoption (hatched bars). Adopting pairs shown are those that adopted in the colony and donors are pairs whose chicks became unforced adoptees in the colony. Pairs that were both adopters and donors (n = 11) are excluded. Sample sizes are in parentheses. The number of chicks hatched did not differ among adopting, non-adopting, and donor pairs (Kruskal-Wallis $H = 3.350$, $df = 2$, $p = 0.1873$), whereas adopting pairs had larger broods at departure from the nesting island than either non-adopting pairs or donor pairs ($F_{2,235} = 52.471$, $p < 0.0001$, Tukey-Kramer $q > 1.154$, $q_{critical} < 0.624$, $p < 0.0001$ for each of the three comparisons).

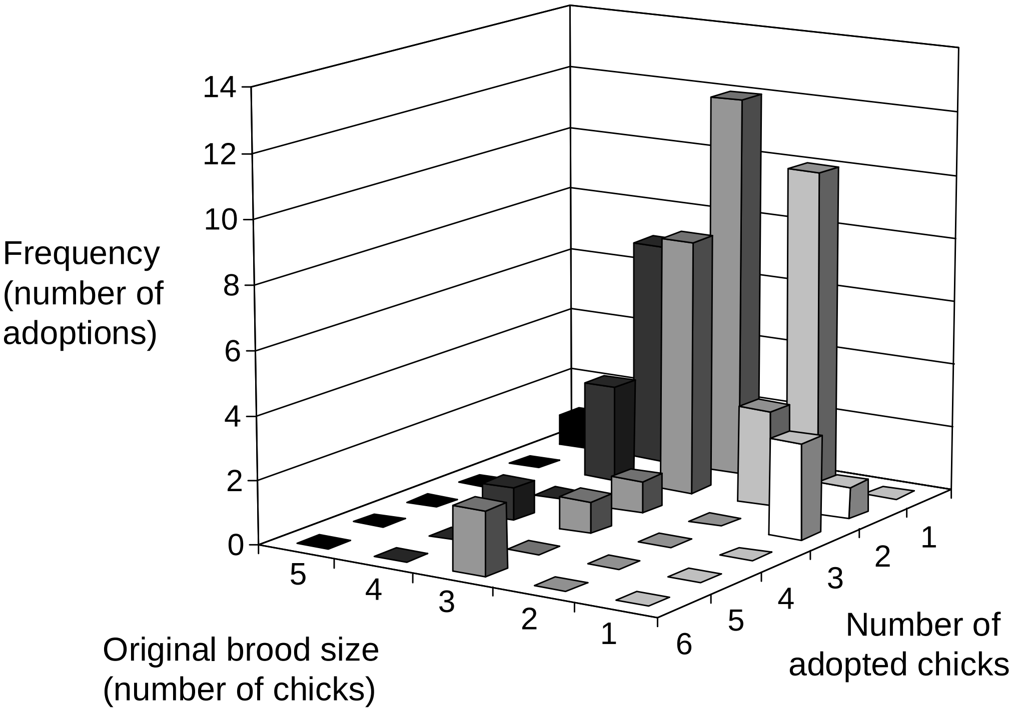
Figure 4. Mean (± S.E.) number of young fledged per brood as a function of brood size. Both adopted chicks and resident chicks were included in this analysis. Sample sizes (number of broods) are in parentheses. More young fledged from larger broods than from smaller broods (Kruskal-Wallis $H = 21.501$, $df = 4$, $p = 0.0003$).

Figure 5. Mean (± S.E.) prey density on territories of adopting, non-adopting and donor pairs. Prey density was quantified by the residuals of a one-way ANOVA in which year was the main effect and the log-transformed number of aquatic macroscopic invertebrates per liter water was the response variable. The difference between adopting and non-adopting pairs was significant ($F_{2,60} = 4.489$, $p = 0.0152$, Tukey-Kramer $q = 0.359$, $q_{critical}= 0.288$, $p < 0.05$).

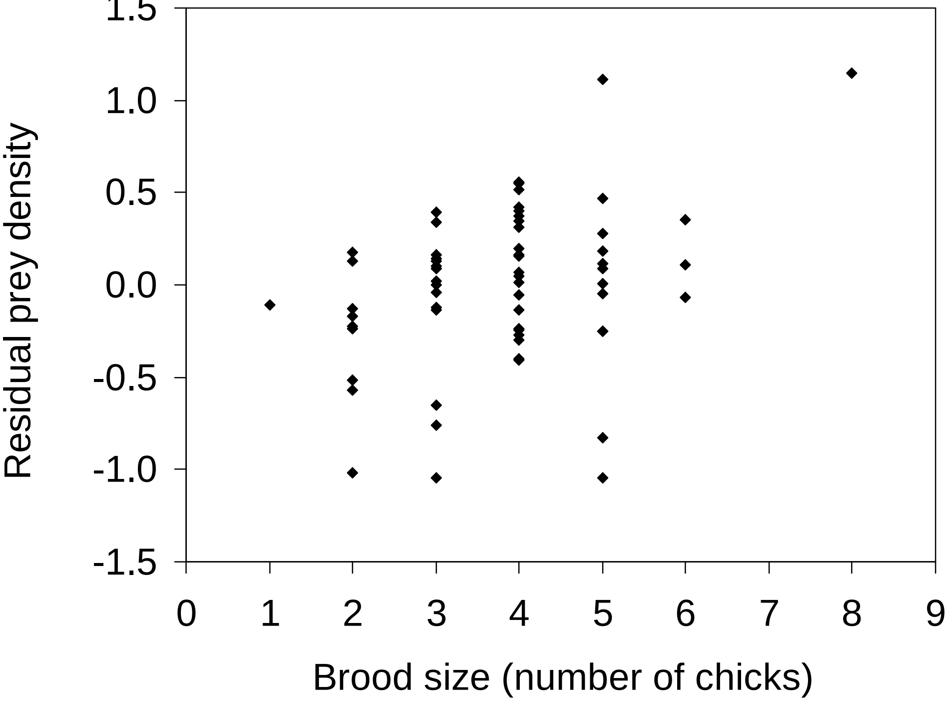
Figure 6. Mean (± S.E.) number of young fledged per brood by the adoption status of parents and by brood size after adoption. Only resident chicks (the parents' own young) were considered in the number of fledged young. Numbers above bars are sample sizes (number of broods). Both adoption status and brood size influenced the number of young fledged (two-way ANOVA, adoption status: $F_{2,225} = 3.835$, $p = 0.0230$, brood size: $F_{4,225} = 2.714$, $p = 0.0308$, interaction: $F_{4,225} = 0.744$, $p = 0.5629$).

Figure 7. Hatching order and mean (± S.E.) body size of chicks. Body size was quantified by factor scores (PC1) computed by a Principal Component Analysis of three primary variables of chick body size (culmen length, tarsus length, body mass). First-hatched chicks were significantly larger than fourth-hatched chicks ($F_{3,252} = 3.074$, $p = 0.0283$, Tukey-Kramer $q = 0.500$, $q_{critical}= 0.448$, $p < 0.05$).

Chapter 3, Figure 1.



Chapter 3, Figure 2.



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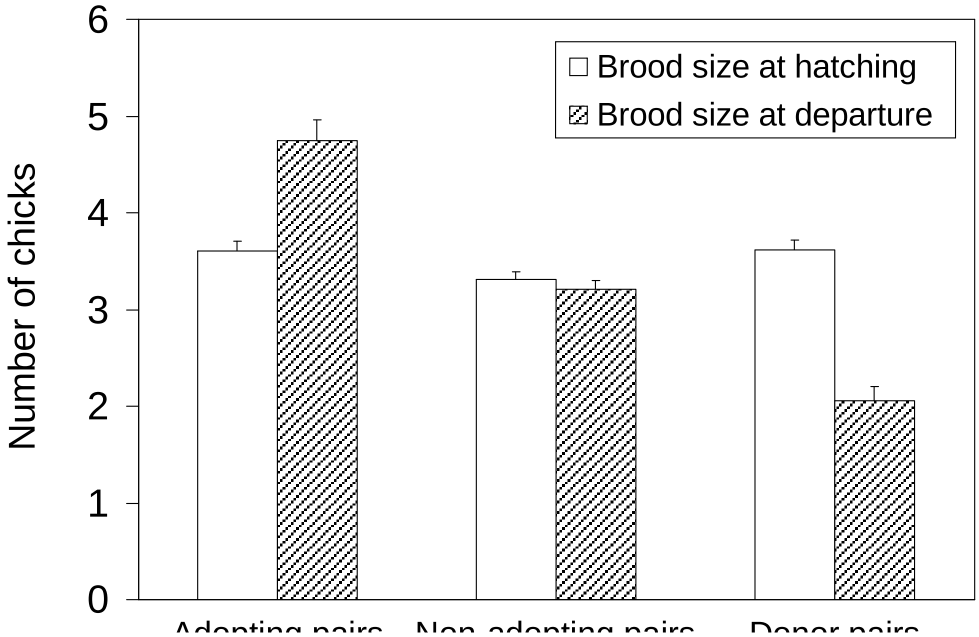

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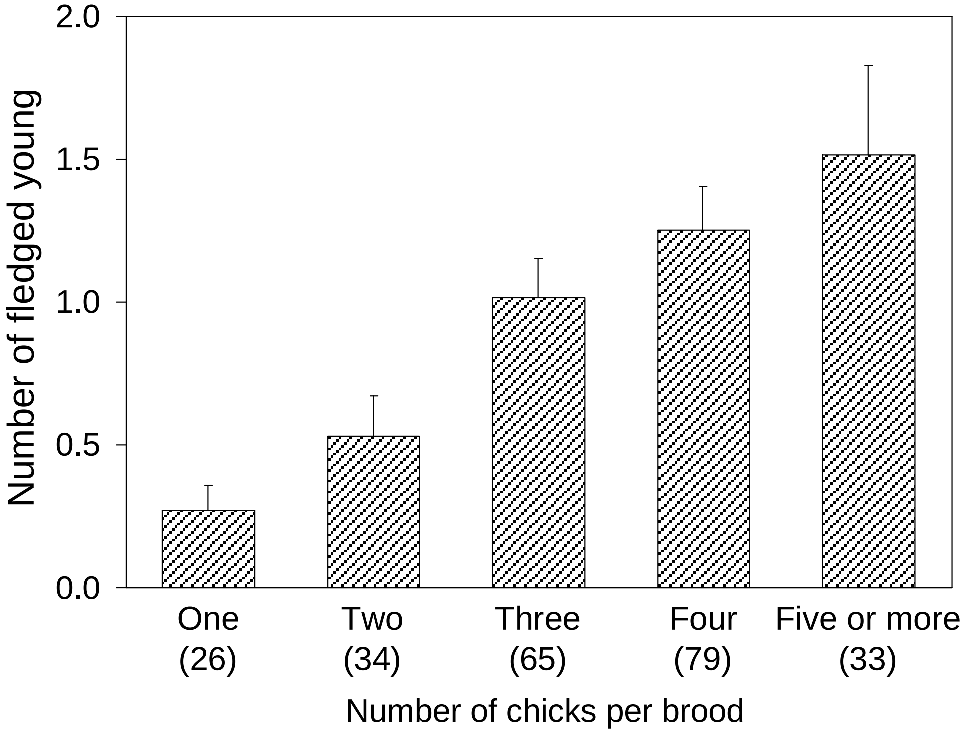

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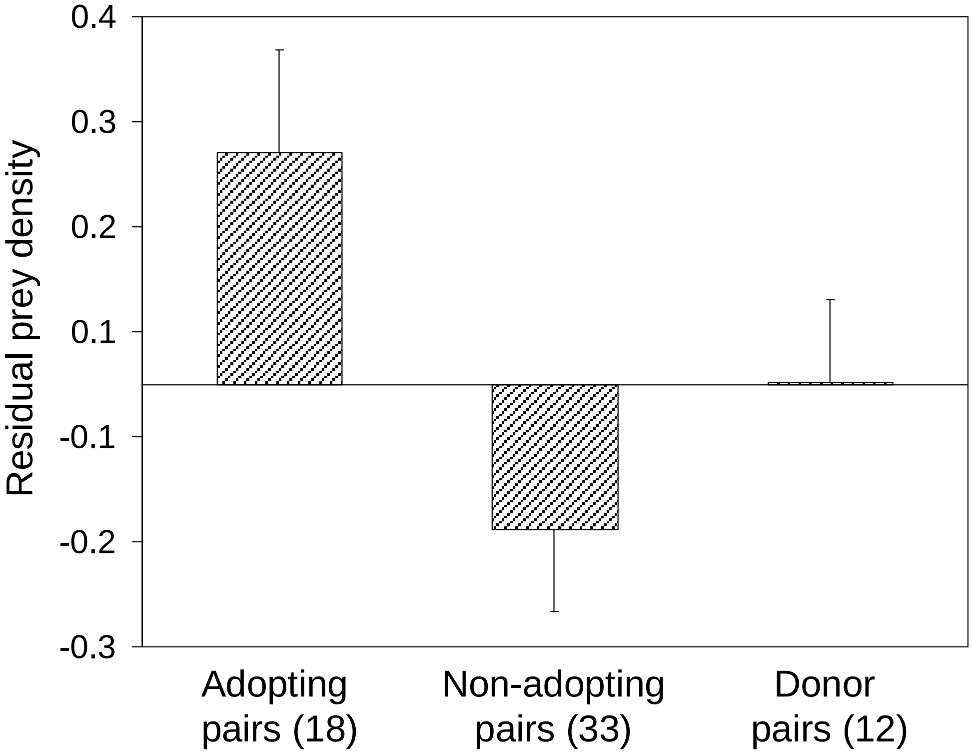

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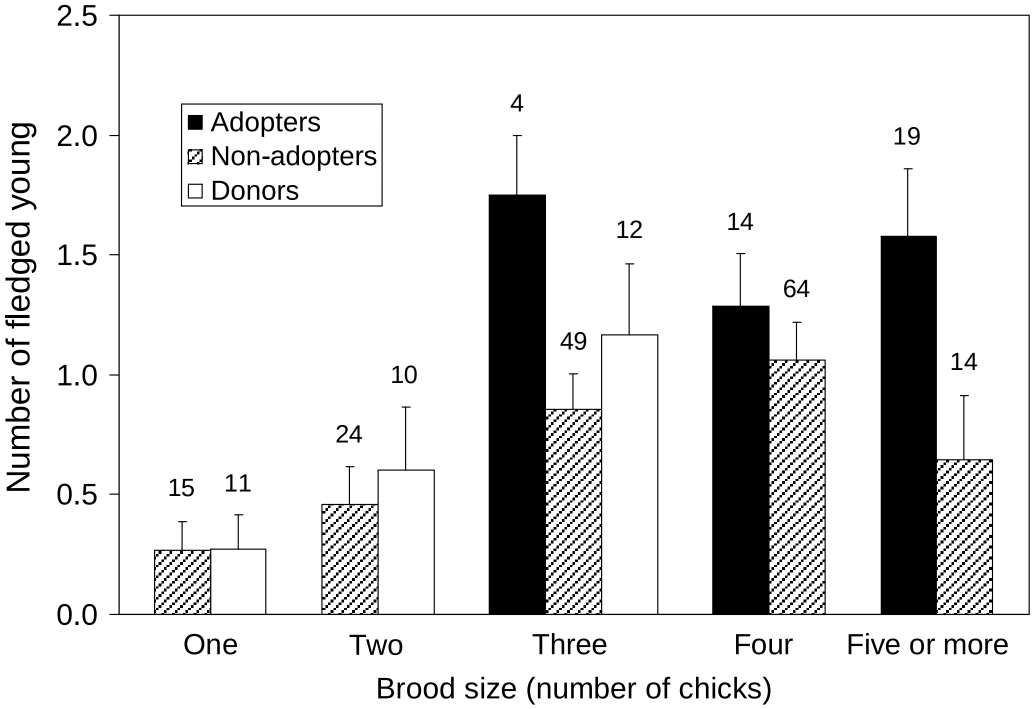

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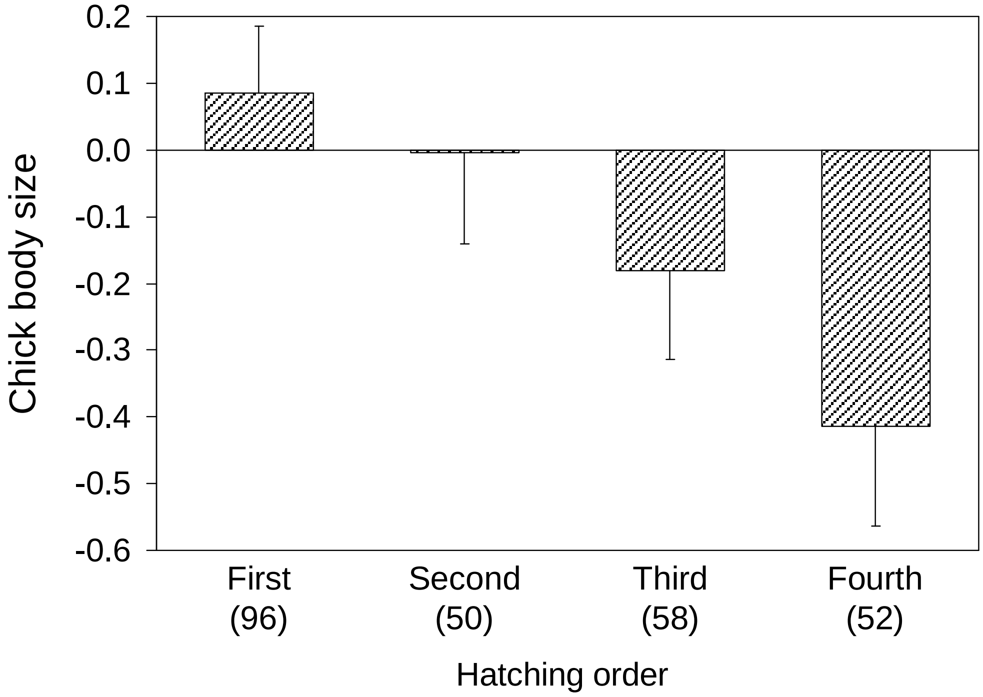


CHAPTER 4. ADOPTION AND THE COSTS OF REPRODUCTION IN AVOCETS

4.1. INTRODUCTION

Natural selection should favor individuals that can maximize their lifetime reproductive success. Physiological and behavioral costs set a limit on how many offspring parents can successfully rear to weaning or fledging, and animals may produce an optimal number of young to maximize their reproductive success (Lack 1968). Two hypotheses have been proposed to explain the trade-off between maximizing reproductive success and the costs of reproduction in birds. First, the energetic demands of producing eggs may limit the number of eggs the females can lay (egg production-limitation hypothesis). Alternatively, the energetic demands of caring for eggs and/or young may limit the number of offspring the parents can successfully hatch and rear to fledging (parental provisioning-limitation hypothesis). These hypotheses have been tested by numerous studies in passerine birds (see reviews by Klomp 1970; Godfray et al. 1991; VanderWerf 1992; Stearns 1992). Much less is known about the factors influencing optimal clutch and brood size in non-passerine taxa (Winkler & Walters 1983).

Shorebirds have long intrigued researchers interested in optimal clutch size because clutch size is highly constant in this ecologically and behaviorally diverse group (Winkler & Walters 1983; Székely et al. 1994; Sandercock 1997). Clutch size in shorebirds may be limited by the ability of parents to successfully incubate large clutches (Lack 1947). Two experimental studies found evidence for the incubation ability hypothesis (Hills 1980; Delehanty & Oring 1993). Other experiments provided only partial support for this hypothesis (Shipley 1984; Székely et al. 1994; Yogev et al. 1996; Sandercock 1997). Costs of larger than normal clutches include increased rates of clutch abandonment, partial clutch loss, longer incubation period and higher risk of predation, hatching asynchrony, and reduced hatchability and egg viability (Arnold 1999). Most of the above studies have focused mainly on incubation and hatching success, and less on brood-rearing and fledging success. The lack of information from the brood-rearing phase, which may be caused by the difficulty of measuring fledging success in shorebirds, may lead to an overestimation of the actual fitness by simply looking at hatching success.

Here, I measured the fitness costs and benefits of enlarged clutches and broods during both incubation and brood-rearing in a colonially nesting shorebird, the Pied Avocet (*Recurvirostra avosetta*). I used annual breeding success as a measure of fitness for adults and survival until fledging as a fitness-measure for chicks. To test whether avocets are capable of successfully incubating extra eggs in their clutch, I experimentally added one or two eggs to normal clutches. The experiment controlled for the potentially confounding effect of adult quality by randomization, and for the effect of laying date by manipulating some clutches earlier and some clutches later in the nesting season.

In avocets, there is a positive correlation between brood size and number of young fledged per brood (Chapter 3). Pairs that adopt alien chicks fledge more of their own young than pairs that do not adopt chicks (Chapter 3). Furthermore, higher-quality parents are more likely to adopt than lower-quality parents (Chapter 3). To separate the effects of adoption and brood size on fledging success, I manipulated the size and composition of broods and controlled for adult quality by randomization in two experiments. These experiments can help in understanding the costs of reproduction and the role of adoption in the breeding and social system of avocets.

4.2. METHODS

4.2.1. General field methods

Fieldwork was conducted in a population of avocets breeding on alkaline lakes in the Kiskunság National Park (KNP) in central Hungary, in 1999 and 2000. The Pied Avocet is a middle-sized shorebird breeding in salt marshes and on salt evaporating ponds in coastal areas in Europe and near alkaline or saline lakes inland east of the Black Sea (Cramp & Simmons 1983; Hagemeijer & Blair 1997). Avocets nest in colonies, that often are formed on small islands. The species is monogamous and both parents care for the young. The chicks are fully precocial and are able to walk and feed on their own within a few hours after hatching. More details on the breeding biology of the studied population of avocets are given in Chapter 2.

Nests were located by searching areas used by avocets for nesting. Every nest was numbered, marked and recorded on a schematic map. The length, breadth, and mass of the eggs were measured and eggs were floated to determine incubation stage, from which the expected date of hatching was estimated (Chapter 2). Nests were checked at least once per week, and more often before hatching. Nest fates were determined as described in Chapter 2.

Hatching colonies were searched for young chicks at least once per day. Chicks were measured (culmen length, tarsus length, and body mass) and color-banded less than 24 hours after hatching. Broods were monitored by locating families in the chick-rearing areas. Searches were conducted using a telescope to find vigilant adults and identify their chicks from hunting blinds or a car. The location of the territories and the composition of avocet broods were recorded on habitat maps. A chick was considered fledged, if it was seen at or after age 35 days (when avocet young are able to fly). The death of chicks was usually inferred by their disappearance from broods rather than by direct observation because most mortality occurred by predation, and mostly at night. A more detailed description of field methods is given in Chapter 2.

4.2.2. Behavioral observations

Behavioral observations were conducted to estimate the time budgets of both adults and young in as many broods as possible. Observations were made when a brood was first seen to occupy a territory in the brood-rearing areas. Adults and chicks of a brood were observed on different days, with the latter enjoying a priority because the behavior of chicks was more difficult to observe.

Behavioral observations lasted for 30 minutes for both adults and young. Adult behavior was recorded continuously by measuring the time spent with each behavior using a stopwatch. Adult behavior types included self-maintenance behavior (feeding, preening, resting, walking), and parental behavior (brooding, calling to the chicks, defense against predators, leading, territorial aggression, vigilance).

Chick behavior was recorded instantaneously for every chick once every minute for 30 minutes. Chick behavior included being brooded, feeding, preening, resting, and vigilance. In every 5th minute, I also recorded the distance between the vigilant parent and every chick separately. I estimated distance by using the height of the vigilant parent (approximately 40 cm) as a template.

4.2.3. Clutch size manipulation

4.2.3.1. Objective and experimental design

The clutch enlargement experiment was conducted to test whether incubating a larger clutch incurs costs or benefits to adults and whether these costs and benefits influence parental investment and chick survival during the brood-rearing period. In this experiment, I increased the number of eggs in clutches at different stages of incubation in a completely randomized design. The experimental units were individual clutches, and each clutch and experimental egg was used only once in the experiment. The clutches were randomly allocated to one of two treatment levels, (i) enlarged clutches: clutch size was increased by adding one or two eggs to the nest, or (ii) control clutches: the nest was visited, but no egg was added to it. The response variables were proportion of abandoned clutches, length of the incubation and hatching periods, fate of the clutch, hatching success, body size of chicks, fledging success, and breeding success of parents.

4.2.3.2. Experimental protocol

The experiment was conducted in seven avocet nesting colonies on Kelemen-szék, a 500-ha, shallow alkaline lake near Fülöpszállás in central Hungary in May and June 2000. Alkaline lakes are the natural breeding habitats of avocets in Hungary. Experimental eggs were collected from avocet nests in drained fishponds threatened with flooding at Biharugra, eastern Hungary (ca. 200 km from the study sites) and at Szeged-Ferto (ca. 100 km). Eggs were transported in paper boxes that were kept warm during the process to prevent the death of embryos. Eggs were floated in water to determine their stage of incubation (Chapter 2). I selected experimental clutches randomly from a pool of clutches that were in the same incubation stage as the eggs. Nests that were not selected in the studied colonies automatically became controls. The eggs then were transferred to and put into the nests. Two eggs were placed in the same nest when there were not enough clutches at the appropriate stage of incubation (within 1-2 days). Control clutches were also visited during the manipulation, but no eggs were placed in them. The manipulation was conducted twice during the season, the first batch (n = 28 clutches) was started on May 8, 2000, when the earliest clutches were about halfway through their incubation, and the second batch (n = 38 clutches) was started on May 18, during the second peak of clutch initiations (Chapter 2).

Avocets are known to incubate clutches larger than the usual four eggs (Hötker 2000). In my study, 2.3% of the clutches known to be complete (n = 597) contained five eggs and two clutches (0.3%) had six and seven eggs, respectively (Chapter 2). After the manipulation took place, adults with enlarged clutches initially interrupted incubation several times and tried different incubating positions apparently to cover as many eggs as they could. However, after 10-15 minutes incubation resumed in a normal manner and the incubation behavior (posture, interruptions) of adults with enlarged and unmanipulated clutches could not be distinguished. In all, 66 clutches were enlarged and 109 clutches were used as controls.

4.2.4. Brood manipulation experiment

4.2.4.1. Objective and experimental design

The brood manipulation experiment was carried out to test the effects of adoption and brood size on breeding success while controlling for potential confounding effects, such as parental and chick quality. In this experiment, I manipulated the composition and size of broods in a one-factor completely randomized design. The experimental units were avocet broods, and each brood and experimental chick was used only once in the experiment. The broods were allocated to one of the following three treatment levels randomly: (i) enlarged broods: one alien chick was added to the brood, (ii) modified broods: one alien chick was added to the brood and a randomly chosen resident chick was taken away from the brood, and (iii) control broods: these broods were disturbed in the same way as were enlarged and adoptive broods, but no chick was added or taken away. These treatments were applied to separate the effects of adoption *per se* and brood size. The response variables were probability of fledging, number of fledged young, and behavior of adults and chicks.

4.2.4.2. Experimental protocol

The experiment was conducted in two natural habitats of avocets (alkaline lakes Bába-szék and Kelemen-szék) and in two artificial habitats (a fishpond near Akasztó and a reconstructed wetland near Fülöpszállás) in May and June 1999. On daily visits to hatching colonies, I first determined the number of hatching nests and hatched young, and banded and measured all chicks found. Then I randomly assigned broods into one of the treatment levels described above. To increase the chance that the experimental chick is part of the brood, experimental broods were chosen only if they contained newly hatched chicks which were still wet and had their egg-tooth, and which were unlikely soon to be led away from the nest by their parents. Next, I randomly selected experimental chicks. For modified broods, I randomly selected which chick was to be taken away from the brood and used these chicks in the manipulations. If it was necessary, I also used chicks from other, randomly chosen broods which were not otherwise part of the experiment. In the final step, I transferred the chicks taken away from their own brood to the randomly selected experimental broods.

Artificial adoptions were considered successful if the experimental chick was observed in the experimental brood after the manipulation. If the experimentally adopted chick did not stay with the experimental brood after the manipulation, the treatment was cancelled for that brood. Other changes in treatment occurred when the experimental brood naturally adopted one or more chicks. If a control brood naturally adopted chicks, its treatment was cancelled (n = 2 broods). If a modified brood adopted another chick (n = 3 broods), its experimental treatment was changed to “enlarged” because brood size had increased, whereas if enlarged broods adopted (n = 5), the treatment category was left unchanged. In all, 26 broods were enlarged, 24 broods were modified, and 26 broods were controls.

4.2.5. Statistical analysis

Because experimental eggs were of various ages, clutches were manipulated at different stages of incubation. Approximately half (47%) of the manipulated clutches (n = 66) were enlarged at an early stage of incubation (< 3 days after laying of the last egg), whereas 26% were manipulated 6-8 days, and 27% were manipulated 12-16 days into incubation (mean ± S.D. length of the incubation period is 22.9 ± 1.19 days). None of the response variables differed by which stage of incubation the manipulation occurred (Kruskal-Wallis tests, $p > 0.24$), therefore, I combined data from the different stages of incubation.

Incubation period was calculated only if the exact start of egg-laying was known, and incubation period was measured as the number of days between the laying of the last egg and the hatching of the first natural egg. Hatching period was given by the number of days between the day of hatching of the first chick (inclusive) and the day of hatching of the last chick (exclusive) within a clutch.

In analyses of fledging success in the brood manipulation experiment, I separated artificial and natural habitats because fledging success was known to differ considerably between the two habitats (Chapter 2). I used non-independent contrasts for post-hoc comparisons of fledging success and adjusted the experimentwise error rate by the Dunn-Sidák method (Sokal & Rohlf

1995). In the brood manipulation experiment I used data on the date of laying, clutch size, and hatching success to quantify the quality of parents and to check whether adult quality was random with respect to the treatment levels.

Parametric statistical tests were used only if the assumptions of such tests were met by the data. In other cases, I used arcsine-squareroot-transformation for behavioral percentages or applied non-parametric tests for other variables. Means ± 1 S.D.s are given throughout the paper unless noted otherwise and two-tailed statistical probabilities are reported.

4.3. RESULTS

4.3.1. Clutch enlargement experiment

4.3.1.1. Clutch enlargement treatment

Sixty-six clutches were experimentally enlarged by adding one (n = 59 clutches) or two eggs (n = 7) in seven colonies, and 109 clutches in the same colonies were used as controls. Experimental clutches became significantly larger than control clutches after the manipulation (Table 1.).

4.3.1.2. Clutch abandonment and clutch predation

One enlarged clutch (1.5%, n = 66 clutches of known fate), and five control clutches (4.6%, n = 109), were abandoned by the incubating adults after the manipulation (Fisher's exact p = 0.4112). Another 12 experimental clutches (18.2%) and 18 control clutches (16.5%) were completely taken by predators (mostly foxes, badgers and harriers) before the expected date of hatching (Fisher's p = 0.8393). Finally, the cause of loss could not be determined for one experimental clutch.

4.3.1.3. Incubation period and hatching asynchrony

There was no difference in incubation period between experimental (22.8 ± 1.68 days, n = 31 clutches with known incubation periods) and control clutches (22.8 ± 1.12 days, n = 23, t = 0.678, df = 52, p = 0.5010). There was also no difference in incubation period between clutches enlarged in early May (22.6 ± 1.56 days, n = 14) and those enlarged in mid-May (23.1 ± 1.78, n = 17, t = 0.801, df = 29, p = 0.4295).

Experimental clutches took longer (2.2 ± 0.79 days, n = 52) to hatch than control clutches (1.9 ± 0.68, n = 86, t = 2.055, df = 136, p = 0.0418). There was also no difference in hatching period between clutches enlarged in early May (2.1 ± 0.77 days, n = 21) and those enlarged in mid-May (2.3 ± 0.82, n = 31, t = 0.163, df = 50, p = 0.4730).

4.3.1.4. Hatching success

The proportion of clutches that hatched at least one chick was 81.8% for experimental clutches (n = 66 clutches of known fate), and it was 78.9% for control clutches (n = 109) (Fisher’s p > 0.6999). In two experimental clutches, only the experimental egg hatched (n = 1 egg in both cases). Within experimental clutches, there was no difference in probability of hatching chicks between clutches manipulated in early May (78.6%, n = 28 clutches), and those manipulated in mid-May (84.2%, n = 38) (Fisher’s p = 0.7481). There was also no difference in the probability of hatching between clutches enlarged by one egg (79.7 %, n = 59) and those enlarged by two eggs (100%, n = 7) (Fisher’s p = 0.3340).

More young hatched from experimental clutches than from control clutches (Table 1.). The proportion of eggs hatched did not differ between enlarged and control clutches (Table 1.). The number of chicks that hatched from clutches manipulated in early May was 4.1 ± 0.97 (n = 22 clutches hatching chicks), whereas 4.0 ± 1.52 chicks hatched from clutches manipulated in mid-May (n = 32) (Mann-Whitney U = 322.0, p = 0.5760). There was also no difference in the number of young hatched between clutches enlarged by one egg (4.0 ± 1.25, n = 47) and those enlarged by two eggs (4.0 ± 1.83, n = 7, Mann-Whitney U = 163.0, p = 0.9674). The proportion of eggs from experimental clutches was similar for the early May and mid-May manipulations (early May: 93.6 ± 17.24%, n = 22, mid-May: 84.9 ± 26.22%, n = 32, t = 1.359, df = 52, p = 0.1800). The proportion of eggs hatched was 89.7 ± 22.67% in clutches enlarged by one egg (n = 47) and 79.8 ± 26.73% in clutches enlarged by two eggs (n = 7, Mann-Whitney U = 113.5, p = 0.0877). Eggs that did not hatch were left by parents in the nest.

In 20.4% of the experimental broods (n = 49 broods of known fate), one or more chicks died immediately after hatching, whereas only 3.8% of the control broods (n = 78) lost chicks to death in or near the nest (Fisher's exact probability = 0.0049). The chicks lost at the nest (16 chicks at 13 experimental and control nests) did not show injuries or other clues of mortality. However, abnormal chick development, indicated either by the legs pointing outward (4 chicks) or by an open yolk sac (1 chick), could be confirmed in several cases. There was no difference between experimental broods (n = 49) and control broods (n = 78) in the probability of other types of chick loss at the nest (leaving live chicks behind at the nest, experimental: 6.1%, control: 12.8%, Fisher's p = 0.3676, chicks departing from the brood, experimental: 22.4%, control: 21.8%, Fisher's p > 0.9999).

The body size of chicks at hatch did not differ between broods hatched from experimental and control clutches (Table 2.). The body size of chicks did not affect their survival (Chapter 2).

4.3.1.5. Costs and benefits during brood-rearing

Even though 20.4% of the experimental broods had chicks die at the nest, broods hatching from experimental clutches had more chicks when they left the nesting island (3.8 ± 1.33 chicks, n = 54 broods) than broods hatching from control clutches (3.3 ± 0.93, n = 86, Mann-Whitney U = 1613.5, p = 0.0015).

Pairs with experimental and control broods were equally likely to adopt alien chicks. The proportion of adopting broods was 18.9% for experimental broods (n = 37 broods of known adoption status), and 25.0% for control broods (n = 68) (Fisher's p = 0.6277). Experimental broods in which chicks died at the nest were not more likely to adopt (20.0%, n = 10) than experimental broods not losing chicks to death (18.5%, n = 27, Fisher's exact $p > 0.9999$).

Pairs with experimental broods (n = 19) held territories with a prey density of 94.4 ± 103.32 aquatic macroinvertebrates per liter water whereas the prey density on territories of pairs with control broods (n = 24) was 120.2 ± 69.54 aquatic organisms per liter (Mann-Whitney U = 143.0, p = 0.0376).

Pairs with experimental and control broods spent similar proportions of their time performing parental behavior (Table 3.). However, pairs with experimental broods spent more time feeding than did pairs with control broods (Table 3.).

The proportion of experimental broods fledging at least one chick was 46.9% (n = 49 broods of known fate), whereas 50.0% of the control broods (n = 78) fledged chicks (Fisher's p = 0.8555). Pairs with experimental broods (n = 49) fledged 0.8 ± 0.98 chicks, whereas pairs with control broods (n = 78) fledged 0.9 ± 1.15 chicks (t = 0.564, df = 125, p = 0.5740, naturally adopted chicks were excluded). There was also no difference in the number of fledged young per brood when brood size was included in the model as a factor and the effect of season (Chapter 2) was controlled for by using julian date of laying as a covariate ($F_{\text{manipulation}} = 0.018$, df = 1, $df_{\text{residual}} = 120$, p = 0.8932; $F_{\text{brood size}} = 3.792$, df = 4, p = 0.0048, $F_{\text{laying date}} = 23.852$, df = 1, $p < 0.0001$).

4.3.2. Brood manipulation experiment

4.3.2.1. Brood size treatment

All pairs accepted experimental chicks because I never observed adults behaving aggressively towards transferred chicks, and the transferred chicks were seen in the experimental brood after the manipulations took place. In two cases, the experimentally adopted chick did not stay in the experimental brood and was seen with another brood (treatment was cancelled in these cases). Enlarged broods had 4.8 ± 1.02 chicks (n = 26 broods, range 3 – 7 chicks), modified broods had 3.6 ± 0.71 chicks (n = 24, 2 – 5), and control broods had 3.4 ± 0.75 chicks (n = 26, 2 – 4) ($F = 21.112$, $df_{treatment} = 2$, $df_{residual} = 73$, $p < 0.0001$, Tukey-Kramer $q > 1.183$, $q_{crit} < 0.560$, $p < 0.05$ for both comparisons of enlarged broods against the other treatment levels).

4.3.2.2. Fledging success

Enlarged, modified and control broods were equally likely to fledge at least one young (Table 4.). However, the number of young fledged per brood differed among treatment levels in artificial habitats (high predation sites) when the effect of brood size was controlled for (Figure 1.A, $F_{treatment} = 3.621$, $df = 2$, $df_{residual} = 51$, $p = 0.0339$; $F_{brood\ size} = 11.589$, $df = 1$, $p = 0.0013$; $F_{interaction} = 2.458$, $df = 2$, $p = 0.0957$). Post-hoc comparisons based on non-independent contrasts showed that broods that had been enlarged fledged more chicks than broods that were not enlarged (modified and control broods combined) ($F = 7.627$, $df = 1$, $p = 0.0080$, $\alpha_{adjusted} = 0.0253$), whereas broods containing experimentally adopted chicks (enlarged and modified broods combined) did not fledge more young than did controls ($F = 3.003$, $df = 1$, $p = 0.0891$, $\alpha_{adjusted} = 0.0253$). There were no differences in the number of fledged young among treatment levels in natural habitats (low predation sites) (Figure 1.B, $F_{treatment} = 0.811$, $df = 2$, $df_{residual} = 13$, $p = 0.4656$; $F_{brood\ size} = 0.449$, df

= 1, $p = 0.5147$; $F_{interaction} = 1.548$, df = 2, $p = 0.2494$). Similarly, there were no differences in the number of young fledged per brood among treatment levels when data from both habitats were combined and when the effects of habitat and brood size on fledging success (Chapter 2) were controlled for ($F_{treatment} = 1.502$, df = 2, $df_{residual} = 71$, $p = 0.2297$, $F_{habitat} = 28.329$, df = 1, $df_{residual} = 71$, $p < 0.0001$, $F_{brood\ size} = 10.903$, df = 1, $p = 0.0015$, for all interactions $p > 0.06$).

The number of resident chicks fledged differed between enlarged and modified broods in natural habitats but not in artificial ones (Table 5.). The probability of fledging for experimentally adopted chicks was similar in enlarged (34.6% of chicks fledged, n = 26) and in modified broods (29.2%, n = 24, Fisher's exact probability = 0.7666), and these proportions were similar in both habitats (Fisher $p > 0.9999$ in both comparisons).

4.3.2.3. Behavior of chicks and adults

The behavior of experimentally adopted chicks did not differ from that of the resident chicks (Table 6.). There was no difference in the time budget of resident chicks in enlarged, modified and control broods (Kruskal-Wallis tests, $p > 0.15$). Experimentally adopted chicks were on average 2.2 ± 1.80 m from the vigilant foster parent, whereas the resident chicks were on average 1.9 ± 1.57 m from their parent (paired $t = 1.593$, df = 10, $p = 0.1422$).

The proportion of time spent with parental behavior did not differ among pairs with enlarged broods (75.2 ± 23.46%, n = 9), modified broods (76.5 ± 27.33%, n = 4) and control broods (75.9 ± 12.14%, n = 6) ($F = 0.005$, df = 2, $df_{residual} = 16$, $p = 0.9950$). This result did not change when brood age and brood size were controlled for ($p > 0.95$). None of the individual behavior types differed among pairs with enlarged, modified and control broods (Kruskal-Wallis tests, $p > 0.14$)

4.3.2.4. Adult quality

There was no difference in the julian date of laying of the first egg among pairs with enlarged, modified and control broods after controlling for differences among colonies ($F = 1.131$, $df = 2$, $df_{residual} = 71$, $p = 0.3286$). Similarly, there was no difference in clutch size ($F = 1.396$, $df = 2$, $df_{residual} = 73$, $p = 0.2541$), or number of chicks hatched ($F = 2.239$, $df = 2$, $df_{residual} = 73$, $p = 0.1138$) among pairs with enlarged, modified and control broods.

4.4. DISCUSSION

4.4.1. Clutch enlargement experiment

Avocets did not appear to incur serious fitness costs, such as clutch abandonment, nest loss or reduction in the number of hatchlings, by incubating larger-than-normal clutches because enlarged clutches hatched on average 0.6 chicks more than did control clutches, which would equal to an 18% difference in annual breeding success. Other results also supported the hypothesis that incubating one extra egg does not reduce hatching success. First, nest abandonment was very rare, and its frequency did not differ between experimental and control clutches. Similarly, no abandonment of enlarged clutches has been reported to occur in American Avocets (*Recurvirostra americana*) (Shipley 1984) and in several other shorebird species (Yogev et al. 1996; Sandercock 1997), although augmented clutches do tend to be abandoned in other shorebirds (Hills 1980; Székely et al. 1994; Delehanty & Oring 1993). Furthermore, I did not detect a difference in the frequency of clutch loss by predation between experimental and control clutches. Second, larger-than-normal clutches were not incubated longer than control clutches. In all other shorebirds studied, enlarged clutches require longer incubation than normal clutches (Hills 1980; Székely et al. 1994; Yogev et al. 1996; Sandercock 1997). Third, experimental and control nests were equally likely to hatch young and the probability of hatching was not influenced by which stage of incubation the manipulation occurred at or whether it took place earlier or later in the season. Fourth, there was no difference in body size between chicks hatched from experimental clutches and those hatched from control clutches. Finally, adults with experimental and control broods had similar time budgets and spent similar amounts of time with parental and self-maintenance behavior after they led their brood to the feeding areas.

Although net hatching success was higher for enlarged clutches than for controls, some results suggested limitations of incubating larger clutches in avocets. First, experimental clutches were enlarged on average by 1.1 egg, whereas they hatched only 0.6 chick more than did controls. Furthermore, clutches that were enlarged by two eggs produced the same number of chicks as clutches enlarged by one egg. Second, enlarged clutches took longer to hatch than control clutches. Asynchronous hatching may increase the exposure of chicks to predation and/or may lead to differences in the developmental stage of chicks, and lower average chick survival within the brood (Stoleson & Beissinger 1995). Third, pairs with broods from enlarged clutches occupied poorer territories and spent more time feeding than did pairs with broods from control clutches. Finally, even though enlarged clutches hatched more chicks, chicks were more likely to die immediately after hatching than chicks hatched in control nests, and there was an increased frequency of developmental abnormalities among the chicks hatched from experimental clutches. These results suggest that some adults may not be able to incubate clutches larger than four eggs successfully or that incubating supernumerary clutches requires extra energy expenditure by parents. However, these results alone are unlikely to indicate selection against supernormal clutches because experimental broods still had on average 0.5 chicks more than did control broods at the time when they departed the nesting colony.

Even though experimental broods were larger than control broods, and brood size positively correlates with fledging success (Chapter 2), experimental broods were not more likely to fledge chicks and did not fledge more young than did control broods. Two mechanisms can explain why the benefits from an extra egg are offset by costs during brood-rearing. First, it is possible that pairs with enlarged clutches invest more heavily into incubating the eggs than pairs with control broods and that the exhaustion of pairs with supernormal clutches prevents them from allocating adequate investment into chicks during brood-rearing. The exhaustion hypothesis is supported by the observation that pairs with experimental broods spend more time feeding than pairs with control broods soon after the broods reach the feeding areas. Alternatively, it also is possible that the difference in brood size (0.5 chick at the departure of broods from the nesting colony) was too small and/or that predation, the main source of chick mortality, was too low in the natural habitat used for the experiment to lead to differences in fledging success (Chapter 2).

In summary, my results provide weak support for the parental provisioning-limitation hypothesis and give indirect support for the egg production-limitation hypothesis. Enlarged clutches did not have increased rates of abandonment or higher risks of predation, were not incubated longer and hatched more young than did control clutches. Enlarged clutches, however, took longer to hatch and were more likely to produce inviable young than controls. Finally, the experimental and control broods produced similar numbers of fledged young. These results indicate that there may be overall costs of incubating supernormal clutches. Other clutch manipulation studies found small fitness costs of enlarged clutches when compared to the potential fitness benefits (25% or 33% for four- and three-egg clutches, respectively) that could be obtained by laying an extra egg (Shipley 1984; Walters 1984; Sandercock 1997). These conclusions, however, have been challenged on the basis that the above studies measured only some of the potential costs and that the different costs could interact in a complex way to limit clutch size in shorebirds (Arnold 1999). Furthermore, the fitness costs and benefits measured in the experiments also can be influenced by factors outside the experimenters' control. In avocets, for example, the fitness costs of larger clutches may be higher in dry years when food is limited than in wet years when food is more abundant.

4.4.2. Brood manipulation experiment

This study provides the first experimental evidence that larger broods may, under some circumstances, fledge more young than smaller ones in shorebirds. The experiment also showed that randomly selected adults could be induced to adopt randomly selected chicks placed in their nests soon after hatching.

The finding that more chicks fledge from enlarged broods than from modified or control broods was significant only in artificial habitats, where predation was high. Pairs that hatch chicks in such habitats (drained fishpond, reconstructed wetland) almost invariably lead their young to feeding areas in natural habitats (shallow alkaline lakes) (Chapter 2). Brood movements, that sometimes involve up to 3-4 km on land, cause high mortality among chicks because they are vulnerable to both aerial and ground predators, and the parents cannot defend the chicks efficiently by themselves (Chapter 2). If larger broods are not preyed upon in higher proportions than smaller broods, then more chicks should fledge in larger broods than in smaller broods because of a dilution of predation among chicks. My results corroborated this prediction because in artificial habitats pairs with enlarged broods fledged on average 0.3 chicks more than did pairs with modified or control broods, which corresponds to a 39% potential increase in fitness compared to control pairs. This result is consistent with previous observations that indicate a positive relationship between brood size and fledging success in avocets (Chapter 2). This result, however, contradicts the findings of the only published brood manipulation study in shorebirds (Safriel 1975). Experimentally enlarged, five-chick broods of Semipalmated Sandpipers (*Calidris pusilla*) are more prone to predation and fledge fewer young than do normal four-chick broods (Safriel 1975). In Safriel's (1975) study, however, larger broods were thought to be more conspicuous and predators were thought to take all young once they discovered a brood. Experimental studies of the relation between brood size and chick mortality in other precocial birds have not found increased chick mortality in enlarged broods (Rohwer 1985; Lessells 1986; Milonoff & Paananen 1993; Loonen et al. 1999).

Factors other than predation may explain why more resident chicks (the parents' own young) fledged in enlarged broods than in modified ones in natural habitats, whereas that difference did not occur in artificial habitats. In natural habitats, brood movements do not involve long treks over land, and therefore, chick mortality caused by predation is less important than in artificial habitats (Chapter 2). In the feeding areas, larger broods tend to occupy better territories than smaller broods, and territory quality and the number of young fledged per brood are positively correlated (Chapter 3). This effect could explain why more resident young fledged from enlarged broods than from modified broods in natural habitats, where predation is less important than in artificial habitats. In several goose and duck species, brood size and dominance are positively related (Boyd 1953; Hori 1964; Raveling 1970; Lazarus & Inglis 1978; Black & Owen 1989a; Williams 1994; Nastase & Sherry 1997), which often results in larger broods accessing better resources than smaller broods (Kehoe 1989; Öst & Kilpi 2000). In Barnacle Geese (*Branta leucopsis*) there is experimental evidence showing that enlarged broods are dominant and occupy better territories than controls (Loonen et al. 1999).

Experimentally adopted chicks fledged in similar proportions in modified and enlarged broods. This result is consistent with observations of natural adoptions, which show that the fledging success of adopted chicks does not vary by the size of the brood into which they gain adoption (Chapter 3).

In summary, larger brood sizes may be beneficial in Pied Avocets both when predation is high and when it is low. When predation is high, chick survival can be higher in larger than in smaller broods as a result of the dilution of predation risks among the chicks. When predation is less intense, other benefits of larger broods may become important. Larger broods, for example, may occupy better territories than do smaller broods, which, in combination with dilution, can further increase the survival of chicks in large broods.

4.4.3. The costs of reproduction and the benefits of adoption in avocets

The results of the clutch manipulation experiment suggest that the benefit of producing more hatchlings by supernormal clutches is offset by a lower chick survival in experimental broods, resulting in experimental and control broods producing similar numbers of fledged young. The lack of overall benefits of an additional egg, and the conservative four-egg clutch, make it likely that the number of hatchlings that can be produced is limited by the number of eggs that can be laid by females. The results of the brood manipulation experiment, however, suggest benefits of larger broods under both high and low predation. Because the number of eggs that can be laid appears to be limited, adoption may be the means to increase the size of the brood for avocets without incurring both the probably substantial cost of producing an extra egg and the slight costs of incubating larger clutches. Thus, selection should favor adoption because it increases the number of genetic young fledged by the adopting pair by increasing the size of their brood. Naturally adopting avocet pairs fledge on average 0.7 chicks more of their own genetic young than do non-adopters, which corresponds to an 84% difference in annual breeding success (Chapter 3). This may explain why adoption of alien chicks occurs frequently, in approximately 21% of the broods in this species (Chapter 3).

If adoption can provide fitness benefits, why is it not more frequent? Previous observational results suggested that adult quality may be important in which pairs become adopters (Chapter 3). This study controlled for the confounding effect of adult quality by randomization, and provided experimental evidence that adoption itself does not lead to an increase in breeding success. This was because the number of young fledged in modified (adopting but not enlarged) broods did not differ from that in control broods. Brood size, thus, is probably more important in explaining the variation in breeding success than adoption *per se*. However, the increase in breeding success resulting from an experimental increased in brood size alone (39%) is less than the 84% difference in breeding success between adopters and non-adopters in natural adoptions. Thus, it appears likely that the effects of adult quality and increased brood size, which both are present in natural adoptions, are both important in explaining the difference in observed fitness between adopters and non-adopters. Adoption, therefore, appears to be beneficial by increasing the size of the brood of high quality adults.

It is possible that both experiments underestimated the potential effect of adoption and the resulting increase in brood size on fledging and breeding success because the average number of chicks adopted in natural adoptions is 1.7 ± 1.16 (range 1-6, Chapter 3), which is 55-70% larger than the original effect size in either experiment (1.1 egg or 0.6 chick in the clutch enlargement experiment and one chick in the Brood manipulation experiment). Therefore, the increase in brood size by natural adoptions may lead to larger changes in fitness than than were caused by the experiments.

In summary, the results of the two experiments appear to support the following hypotheses. Adoption can increase the breeding success of high-quality pairs by increasing the size of the brood, which results in a greater number of genetic offspring fledging. Future studies are necessary to evaluate whether donors obtain benefits or incur costs by losing their chicks to adoption or whether the adopters and adopted chicks are related and benefit from adoption through kin selection.

4.5. TABLES

Table 1. Mean (± S.D.) clutch size and hatching success of experimental and control clutches. Clutch size data shown are for clutches that were known to be complete at manipulation. Sample sizes are in parentheses.

	Experimental clutches	**Control clutches**	**Mann-Whitney U**	**p**
Clutch size before manipulation	4.0 ± 0.13 (61)	4.0 ± 0.35 (98)	2822.0	0.2130
Clutch size after manipulation	5.1 ± 0.44 (61)	4.0 ± 0.35 (98)	286.0	< 0.0001
Number of young hatched	4.0 ± 1.32 (54)	3.4 ± 0.83 (86)	1395.0	< 0.0001
Proportion of eggs hatched (%)	88.4 ± 23.20 (54)	87.3 ± 19.35 (86)	2130.0	0.3195

Table 2. Mean (± S.D.) values of body size variables of chicks hatching in experimental and control clutches. Chicks were measured in less than 24 hours after hatching and data were averaged per brood to avoid pseudoreplication. Sample sizes (number of broods) are in parentheses.

Body size variable	**Experimental clutches**	**Control clutches**	**t**	**df**	**p**
Culmen length (mm)	15.6 ± 0.73 (42)	15.6 ± 0.72 (68)	0.190	108	0.8497
Tarsus length (mm)	32.9 ± 1.16 (42)	33.1 ± 1.18 (68)	0.925	108	0.3568
Body mass (g)	22.5 ± 1.45 (42)	22.6 ± 1.60 (67)	0.545	107	0.5869
Body size (PC1) [a]	-0.15 ± 0.814 (42)	-0.05 ± 0.904 (67)	0.588	107	0.5580
Body condition [b]	-0.06 ± 1.362 (42)	0.02 ± 1.457 (67)	0.292	107	0.7708

[a] Body size scores are factor values obtained by a principal component analysis of the three original body size variables.

[b] Body condition was quantified by the residuals from a regression of body mass on tarsus length using all chicks measured in this study (n = 602).

Table 3. Mean (± S.D.) percentage of time pairs with experimental and control broods spent with each behavior type during 30-min behavioral observations conducted after pairs occupied territories in the feeding area. Sample sizes (number of observed broods) are in parentheses. Percentages do not add up to 100% because only those observations were analyzed for any behavior type in which the given behavior occurred. A total of 12 experimental and 24 control broods were included in the analysis.

Behavior type	Experimental	Control	Mann-Whitney U	p
Antipredatory behavior	2.7 ± 3.26 (4)	2.5 ± 2.49 (5)	9.0	0.8065
Brooding	34.9 ± 41.98 (7)	36.5 ± 31.82 (10)	31.0	0.6963
Territorial aggression	3.7 ± 4.05 (12)	4.3 ± 4.54 (24)	125.0	0.5232
Vigilance	37.7 ± 25.77 (11)	25.0 ± 18.72 (23)	87.0	0.1459
Parental behavior total	66.9 ± 28.84 (12)	59.3 ± 32.25 (24)	111.0	0.2681
Feeding	27.7 ± 7.18 (4)	14.6 ± 23.25 (17)	11.0	0.0394
Preening	7.1 ± 7.21 (11)	10.6 ± 9.35 (19)	79.0	0.2725
Resting	26.1 ± 19.29 (8)	35.1 ± 25.40 (15)	45.0	0.3329
Self-maintenance total	33.1 ± 28.84 (12)	40.7 ± 32.25 (24)	111.0	0.2681

Table 4. The number of broods fledging at least one chick by treatment level and habitat. One chick was added to enlarged broods a few hours after hatch, whereas one chick was taken away from and one chick was added to modified broods; control broods were disturbed the same way, but no chick was added or taken away. In three enlarged broods and two modified broods in artificial habitats only the experimentally adopted chick fledged. The difference in proportions is not significant (data from both habitats combined: G = 0.978, df = 2, p = 0.6133, broods in which only the experimentally adopted chick fledged were excluded).

	Artificial habitats			Natural habitats		
Brood fate	**Enlarged**	**Modified**	**Control**	**Enlarged**	**Modified**	**Control**
Fledged chicks	8	7	7	6	3	7
Did not fledge chicks	11	12	12	1	2	0
Total	19	19	19	7	5	7

Table 5. Mean (± S.D.) number of resident chicks fledged in experimental broods in artificial habitats (high predation sites) and natural habitats (low predation sites). Sample sizes are in parentheses.

Habitat	Enlarged broods	Modified broods	Mann-Whitney U	p
Artificial	0.5 ± 1.02 (19)	0.3 ± 0.58 (19)	177.5	0.9095
Natural	1.7 ± 0.95 (7)	0.6 ± 0.55 (5)	5.5	0.0417

Table 6. Time budgets of experimentally adopted and resident chicks. Data shown are mean (± S.D.) percentages of time spent with the given behavior by chicks during 30 minutes in 12 enlarged or modified broods. Data for resident chicks were averaged per brood. Percentages were arcsine-transformed before analysis.

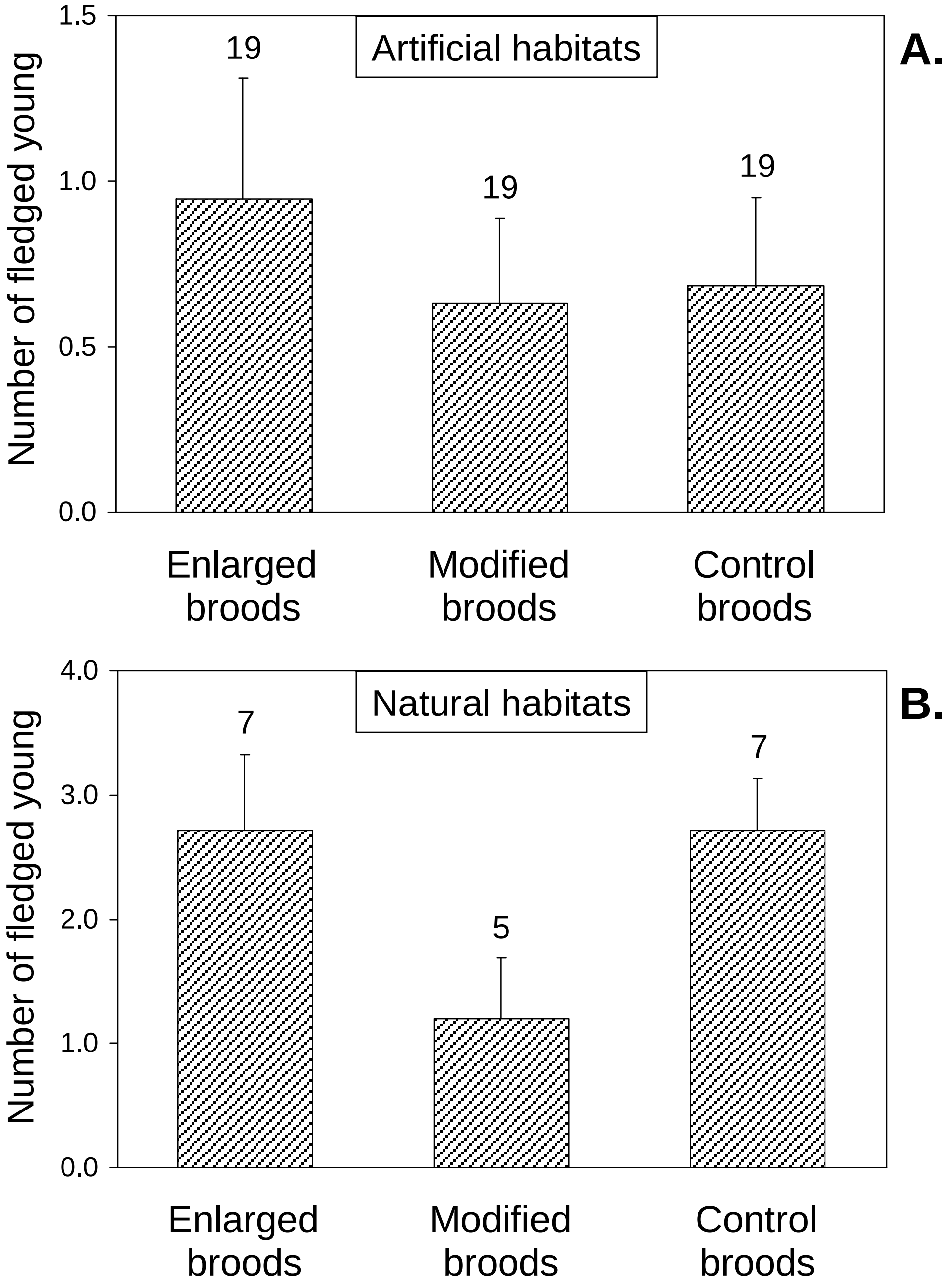
Behavior	Experimentally adopted chick	Resident chicks	t [a]	p
Being brooded	30.2 ± 33.77	27.2 ± 28.95	0.624	0.5454
Crouching	0.9 ± 2.23	0.4 ± 0.99	1.475	0.1681
Feeding	39.6 ± 27.80	40.7 ± 23.41	0.506	0.6225
Locomotion	5.9 ± 5.71	6.7 ± 4.51	1.604	0.1370
Preening	5.0 ± 4.93	7.0 ± 10.84	0.305	0.7661
Resting	18.1 ± 23.89	17.5 ± 24.43	0.446	0.6646
Vigilance	0.2 ± 0.92	0.5 ± 1.25	0.561	0.5863

[a] Paired t-test.

4.6. FIGURE LEGEND AND FIGURE

Figure 1. Mean (± S.E.) number of fledged young per brood by brood manipulation treatment level in artificial habitats (A) and natural habitats (B). Sample sizes (number of broods) are given above bars.

Chapter 4, Figure 1.



CHAPTER 5. THE IMPORTANCE OF ADOPTION IN THE BREEDING AND SOCIAL SYSTEM OF AVOCETS: BENEFITS OF LARGE BROODS FOR GOOD PARENTS?

5.1. INTRODUCTION

The classic definition of parental care is any action taken by parents which increases the survival of their offspring but which also decreases the amount of parental investment available for future reproduction (Trivers 1971). This definition implies that parents face a decision of whether to invest into their current offspring or save some of their own reproductive potential for future reproduction. Therefore, a central question about parental care is how much time and energy should parents invest into their offspring to optimize the number of offspring that can be reared during their lifetime. To answer this question and to understand the evolution of parental care, it is often useful to examine the various modifications, or deviations, of what can be viewed as "normal" parental care in certain species. Alloparental care, in which adults provide care for young that are not genetically related to them, is one of such deviations that may provide useful insight into the allocation of time and energy by parents. Understanding the costs and/or benefits of caring for additional young may throw light on how parents allocate time and energy into their own offspring.

The most frequent form of alloparental care, the adoption of unrelated young, has long been intriguing to biologists because it seems to counter classic Darwinian evolutionary theory. Caring for unrelated young does not contribute to the fitness of adopting adults, and it is reasonable to assume that it decreases the amount of parental investment available for the adopting adults' own offspring. Therefore, natural selection should eliminate, rather than favor, adoption. However, adoption has been reported in 220 bird species (Brown 1987) and in more than 150 mammal species (Riedman 1982). Traditionally, adoption has been explained as a non-adaptive side-effect or as an altruistic behavior on the part of the alloparent. Recent studies of birds, however, found various benefits for either the adopter or the adoptee (Chapter 1).

In several species of waterfowl (ducks and geese of the order *Anseriformes*) adoption has been interpreted as beneficial because chicks in larger broods survive better either through the increased dominance of larger broods over smaller broods (mostly geese, Black & Owen 1989a, Williams 1994, Loonen et al. 1999) or through a dilution of predation (mostly ducks, Munro & Bedard 1977a, Kehoe 1989, Nastase & Sherry 1997). Numerous studies, however, have found no evidence for costs or benefits of adoption and support the view that adoption is neutral (Williams 1974, Titman & Lowther 1975, Patterson et al. 1982, Warhurst & Bookhout 1983, Bustnes & Erikstad 1991, Gosser & Conover 2000). Still some other studies report behavioral costs, e.g. increased vigilance by parents with larger broods (Forslund 1993, Sedinger & Raveling 1990).

Adoption in gulls and terns (order *Charadriiformes*, family *Laridae*) appears to arise from a drive by young, small and disadvantaged chicks to gain adoption into broods where they are the largest chicks (Graves & Whiten 1980, Pierotti & Murphy 1987). Adoption incurs costs for adults because it reduces the number of their own young that can be reared to fledging (Carter & Spear 1986, Pierotti & Murphy 1987, Roberts & Hatch 1994, Brown et al. 1995, Brown 1998). These counteracting interests create an intergenerational conflict (Pierotti & Murphy 1987), and in most species adoption is suggested to result from a reproductive error on the side of the parents (Knudsen & Evans 1986, Pierotti & Murphy 1987, Morris et al. 1991, Brown 1998).

In spite of extensive studies of adoption in waterfowl and gulls and terns, the adoption behavior of precocial birds in other taxa remains virtually unknown. For example, numerous shorebirds (order *Charadriiformes*, families *Scolopacidae*, *Charadriidae*) and galliforms (order *Galliformes*) have been reported to adopt alien chicks (Skutch 1976, Cooper & Miller 1992, Lanctot et al. 1995), however, adoption has never been explicitly studied in these large groups of species.

In this paper, I summarize the results of a field study of adoption in avocets, and propose a hypothesis on the role of adoption in the breeding and social system of avocets. The paper will synthesize observations of natural adoptions and experiments to study the effect of adoption, and will include details on the breeding biology only to the extent necessary to understand the results relevant to adoption. Data reported are means ± S.D.s in the text and means ± S.E.s on graphs.

5.2. RESULTS AND DISCUSSION

5.2.1. Breeding biology

The Pied Avocet is a large-sized shorebird (order *Charadriiformes*, family *Recurvirostridae*). The species has a Palearctic distribution; it breeds from western Europe to the Far East. While in Europe most avocets breed in coastal areas, and use salt evaporation ponds and salt marshes for nesting, throughout the majority of the range avocets use large, inland shallow alkaline lakes for nesting. I studied the westernmost of such inland populations of avocets in south-central Hungary between 1998 and 2000.

The nesting habitats in this population are alkaline lakes, which are extremely shallow waterbodies with a large surface area. The lakes change considerably within and between years based upon precipitation and water levels. Avocets prefer to nest on islands on these lakes, however, they may also use the shorelines for nesting. Avocets nest in colonies, which provide protection from various predators because the birds nesting together chase predators off together. Colonies can be highly synchronous and very dense.

The nest is a simple scrape on the ground more or less lined with some nest materials. Avocets almost always lay four eggs, of which the chicks hatch after 23 days of incubation. The chicks are precocial; they are able to walk, leave the nest and feed on their own a few hours after hatching. Avocet parents lead their young from the nesting sites to feeding areas, where the adults defend territories.

In the course of this study, two-thirds of the chicks were individually marked with color-bands on their legs for identification. Avocet broods were monitored by searching the feeding areas for adults and chicks at least twice per week. A chick was considered fledged if it was seen at or after the age of 35 days, when avocet young are able to fly. A chick was considered dead if it was not seen during three consecutive monitoring occasions.

In summary of the breeding biology of avocets, 50% of the nests hatched at least one young. Nests that were most likely to hatch were those that were initiated in artificial habitats (drained fishpond, reconstructed wetland) early in the season, in colonies of more than 10 pairs. Forty-seven percent of the broods fledged at least one chick, whereas only 26% of the young lived to fledging. Chick survival was very low in artificial habitats, from where parents led their young to natural habitats, where chick survival was somewhat higher. Chick survival was extremely low during the first week after hatching, and the high mortality of chicks appears to limit breeding success in avocets.

5.2.2. Natural history of adoption

The majority (60%) of adoptions occur while the broods are still in the nesting colony. Adoptions are also likely during the movement of the broods from the nesting to the feeding areas, whereas adoptions in the feeding areas are rare.

Adoptions are frequent in dense island colonies in which several pairs hatch their chicks at the same time. During hatching, the parents lead the chicks from the nest to the nearest water on the island, where they defend small territories on which the chicks feed. When a pair finally decides to leave the island for the feeding areas with their young, chicks other than their own may join the family and gain permanent adoption there. These chicks are usually the oldest chicks in their natal brood, and are termed as unforced (voluntary) adoptees, because they leave their natal family at their own will. In some other cases, chicks that are left behind by their parents seek adoption into other families. These chicks are the last to hatch in their natal broods, and are termed as forced adoptees.

In the three years combined, I observed natural adoptions in 53 broods, involving the transfer of 92 chicks, or 1.7 ± 1.16 chicks (range 1 – 6) per adoption event. Overall, 13% of the chicks were adopted, and more than two-thirds (65%) of these chicks were unforced adoptees. The proportion of pairs adopting at least one alien chick was 21%, and was fairly constant in the three years (1998: 16%, 1999: 21%, 2000: 24%).

5.2.3. Proximate costs and benefits of adoption

Observational data collected on natural adoptions provided full support for three of the proximate hypotheses tested, and partial support was found for one hypothesis.

5.2.3.1. Diluting-effect hypothesis

The diluting-effect hypothesis states that larger broods are beneficial for parents, because the chance that their own chick gets preyed upon decreases in larger broods. A second prediction of this hypothesis is that the adopted chicks do not benefit from adoption, because their survival does not differ from that of their siblings.

The diluting-effect hypothesis was supported by three results. First, broods that had at least three chicks were more likely to fledge at least one young than broods that had only one or two chicks (Table 1.). Second, more chicks fledged in larger broods than in smaller ones (Figure 1.). Finally, in spite of the fact that unforced adoptees tended to go to broods larger than their natal brood, unforced adoptees fledged in a proportion (28%, n = 46 chicks) very similar to that of their siblings remaining in the natal brood (29%, n = 76) (Table 2., Fisher's exact $p > 0.9999$). In other words, the survival of adopted chicks did not increase by adoption, and I concluded that chicks did not obtain survival benefits from adoption, and that it is probably the parents who benefit from adoption by diluting the risks of predation within their brood.

5.2.3.2. Adult quality hypothesis

The adult quality hypothesis suggests that only parents of good quality can adopt alien chicks, and that brood size may be a signal to indicate adult quality. I used only indirect measures of adult quality, because direct measurements, such as body size, could not be obtained in the field.

Four observations provided support for this hypothesis. First, pairs that later adopted (n = 41 pairs) laid their first egg 1.9 ± 5.47 days earlier than the mean laying date for all pairs, whereas pairs that did not adopt (n = 163) laid eggs 0.4 ± 6.87 days after the mean laying date, and donor pairs (n = 36) laid eggs 2.6 ± 5.43 days before the mean laying date (Kruskal-Wallis test of julian laying dates adjusted for year and colony effects, $H = 10.241$, $df = 2$, $p = 0.0060$). The start of egg-laying is likely to be positively correlated with adult quality in avocets because nest sites within a colony are decided during intense territorial fights. Second, the density of potential prey (waterbugs and chironomid larvae) was significantly higher on territories of adopters than on non-adopters (Figure 2., Prediction 5 supported). Moreover, there was a positive correlation between the number of young fledged per brood and prey density ($r = 0.491$, $n = 63$, $p < 0.0001$). Third, adopters were more likely to fledge at least one of their own chicks than were non-adopters or donors, because 81% of the adopting pairs ($n = 37$) were successful, whereas only 44% of non-adopters ($n = 166$) and 47% of donors fledged young ($G = 17.929$, $df = 2$, $p = 0.0001$). Finally, adopters fledged significantly more of their own young (1.5 ± 1.02 chicks, $n = 37$ broods) than did either non-adopters (0.8 ± 1.08, $n = 166$) or donors (0.7 ± 0.90, $n = 34$) ($F_{2,234} = 6.845$, $p = 0.0013$, Tukey-Kramer $q > 0.309$, $q_{critical} = 0.309$, $p < 0.05$, Prediction 7 supported). When brood size was included in the model as a factor, both adoption status and brood size were significant, while their interaction was not (Figure 3.). These results indicate that adopters are likely to benefit from increased brood sizes by fledging more of their own young (Prediction 7 supported).

5.2.3.3. Chick salvage strategy hypothesis

The chick salvage strategy hypothesis predicts that chicks that are left behind by their parents salvage their survival by gaining adoption into another brood. Another prediction is that adoption is not costly for the foster parent.

Chicks that were left behind by their parents ($n = 21$ chicks, Table 2.) salvaged their chances of survival by being adopted. Eight of these chicks (38%) fledged, and their fledging success was not different from that of their siblings departing earlier with the natal brood (44%, $n = 36$, Fisher's $p = 0.7824$). Therefore, I concluded that these chicks salvaged their survival by gaining adoption. The second prediction was also fulfilled because foster parents did not fledge fewer young than non-adopters; in fact, adopters fledged more of their own young than did non-adopters.

5.2.3.4. Brood dominance hypothesis

The brood dominance hypothesis predicts that pairs with larger broods are more dominant over and can occupy better territories than smaller broods, and thus, there may be a positive relationship between brood size and territory quality.

Behavioral observations conducted after broods settled in territories suggested that the behavior of adults did not change with brood size. However, there was a positive correlation between brood size and prey density on the territory (Figure 4.). Therefore, I concluded that parents with larger broods occupied better territories.

In summary, adopters appeared to benefit from adoption, because pairs with larger broods fledged more young than did pairs with smaller broods. However, adult quality is also important, because adopting pairs laid their eggs earlier, occupied better territories and fledged more young than did non-adopting pairs. Adopted chicks did not seem to obtain any benefits or incur any costs. Chicks that were abandoned by their parents, however, appeared to benefit by gaining adoption into other broods because they achieved a survival similar to that of their siblings remaining in the natal brood. I did not find fitness costs of adoption for the foster parents, and both the diluting-effect and adult quality hypotheses were supported by several pieces of evidence. To separate the effects of brood size and adult quality I conducted two experiments in which either clutch size or brood size were manipulated and adult quality was controlled for by randomization.

5.2.4. Experimental adoptions

5.2.4.1. Clutch manipulation

In this experiment I added one or two eggs to randomly selected nests, and left some nests unmanipulated as controls. The clutch manipulation significantly increased the number of eggs in experimental clutches, from 4.0 ± 0.35 (n = 98 clutches) to 5.1 ± 0.44 eggs. The number of young that hatched from these clutches was higher (4.0 ± 1.32 chicks, n = 54) than the number of young hatching from control nests (3.4 ± 0.83, n = 86, Mann-Whitney U = 1395.0, $p < 0.0001$). This result indicated that apparently there was no effect of clutch enlargement on the number of eggs that can be incubated successfully by avocets. Some costs, however, were obvious, because clutch size was increased on average by 1.1 eggs, whereas the number of hatchlings was only 0.6 higher, indicating that the extra egg hatched in roughly half of the clutches.

Other costs of incubating supernormal clutches included a higher frequency of chick death near the nest. I found one or more dead chicks near 20.4% of the enlarged clutches (n = 49) and near only 3.8% of the control clutches (n = 78) (Fisher's exact p = 0.005). Some of the chicks that died near the nest showed signs of abnormal chick development, including legs pointing outward making walking impossible (n = 4 chicks) or open yolk sac (n = 1).

Even though broods from enlarged clutches were larger at the departure from the nesting island (Figure 5.), and observations suggested a positive correlation between brood size and prey density (Figure 4.), pairs with enlarged clutches occupied territories of lower prey density than did pairs with control clutches (Figure 6.). In a line with this result, pairs with enlarged clutches spent more time feeding in 30-minute behavioral observations than did pairs with control clutches (Figure 7.).

The final evidence of some sort of cost of incubating larger clutches is that there was no difference in the number of young fledged between broods from enlarged and from control clutches (Figure 5.). This is surprising because observational data suggested that the number of fledged chicks is positively related to brood size.

In summary, the clutch manipulation experiment provided several insights into the costs of reproduction in avocets. The immediate costs of incubating supernormal clutches were probably small, because more chicks hatched from enlarged clutches than from control clutches. However, chicks died near enlarged clutches more often than near control clutches, and pairs with enlarged broods occupied poorer territories, and spent more time feeding than pairs with control broods. These results are consistent with the hypothesis that incubating larger clutches requires a higher energy expenditure by parents during incubation, which may result in exhausted parents occupying poorer territories, and spending more time feeding than pairs with control clutches.
Finally, pairs with enlarged broods did not fledge more chicks than pairs with control clutches, even though brood size and the number of fledged young were positively related in the observational part of this study.

To eliminate the costs of incubating extra eggs, I manipulated the number of chicks in certain, randomly selected broods immediately after hatching, and controlled for the effect of adult quality by randomization.

5.2.4.2. Brood manipulation

In this experiment, I added one chick to “enlarged” broods and replaced one chick in “modified” broods, whereas control broods were not manipulated.

More young fledged from enlarged broods than from modified or control broods in areas of high predation pressure (Figure 8.A). On average 0.9 chicks fledged from enlarged broods, whereas 0.6 chicks fledged from modified and control broods fledged. Therefore, I concluded that under high predation pressure the effect of brood size is important in determining the number of fledged young, regardless of the quality or experience of the parents. In natural habitats, where predation was lower, there was no difference when the total number of fledged young was analyzed (Figure 8.B). However, 1.7 ± 0.95 (n = 7) resident chicks fledged from enlarged broods and 0.6 ± 0.55 (n = 5) resident chicks fledged in modified broods (Mann-Whitney U = 5.5, p = 0.042). The sample size is small, however, the difference was large, because pairs whose broods were enlarged fledged almost three times as many of their own chicks as did pairs with modified broods. The reason for this difference is not clear, but it is possible that under weaker predation, other benefits of larger broods can be important besides the dilution effect. For example, larger broods may have occupied better territories than modified ones. However, there was not enough data on territory quality to test this hypothesis.

In summary, three points are worth noting from the experiments. First, pairs whose clutch was enlarged did not produce more young than did control pairs. Several pieces of evidence suggested that incubating supernormal clutches incurs costs for parents during incubation and in the early brood-rearing period. Second, large broods may be beneficial under high predation, because predation risks can be decreased by increasing the size of a brood. It was not clear why more resident chicks fledged in enlarged broods than in modified ones under lower predation pressure. However, because brood size and prey density was positively correlated in the observational part of this study (Figure 4.), it is possible that enlarged broods occupied better territories than modified broods.

5.3. CONCLUSIONS

Both observational and experimental results support the hypothesis that adoption provides fitness benefits to the adopting parents via an increase in brood size. Data from this and other studies of avocet breeding biology suggest that predation has a strong influence on the breeding and social system of this species. The dilution of predation risks due to an increase in brood size by adoption, therefore, may be an important factor in determining breeding success, and this effect can also influence the social system of the species.

Producing an extra egg and incubating five-egg clutches is another potential way of increasing the number of chicks for parents. However, the costs of producing extra eggs and incubating them successfully are likely to be high in avocets. Because avocets may be limited by these costs in how many eggs they can hatch, adoption can function as a means of increasing the size of the brood. Adults can avoid the potentially high costs of producing and/or incubating supernumerary eggs by adopting chicks soon after hatch. The extra parental investment that additional chicks require is probably low or non-existent, because in avocets, like in most precocial birds, parental investment is shareable (or non-depreciable, i.e., does not change with the number of chicks). Thus, selection should favor adoption because it increases the number of genetic young fledged by the adopting pair by increasing the size of their brood.

If adoption provides benefits to parents in the form of increased brood sizes, why do only 21% of the pairs adopt alien chicks? Two groups of results suggest that the quality of the adults (i.e., age and/or experience) is important in which pairs become adopters. First, observational data showed that adults that later would adopt laid their eggs earlier, occupied better territories and fledged more of their own young than did non-adopting pairs. Thus, adopting adults may have been higher quality adults than were non-adopters. Second, the comparison of parental fitness between natural and experimental adoptions provides indirect evidence for the importance of adult quality. When the confounding effect of parental quality was controlled for in the brood manipulation experiment, adopters fledged 0.3 chicks more than did non-adopters, which corresponds to a difference of 39% in fitness. However, in natural adoptions, adopters fledged 0.7 chicks more, or 84% more young than did non-adopters. Thus, the difference in annual breeding success was twice higher in natural adoptions, when the effects of adult quality and brood size both played a role, than in experimental adoptions, in which adult quality was controlled for. I propose that the difference is best explained by the additional effect of adult quality in natural adoptions, which effect was added to the experimentally confirmed effect of brood size on annual breeding success. The addition of these two effects is consistent with the doubling of the difference in annual breeding success between adopting and non-adopting individuals. Therefore, it is likely that only high quality pairs can adopt alien chicks.

In conclusion, this study and several other, recent, studies (Chapter 1) indicate that adoption, in contrast to previous explanations based on altruism and cooperation, can provide fitness benefits to the adopting adults and to chicks that are left behind by their parents. In avocets, adopting adults increase their fitness by increasing the size of their brood, which appears to be beneficial in several ways (e.g. by diluting the risks of predation on chicks or by occupying territories of higher quality). However, adoption is not for every adult; several correlative results and indirect evidence suggest that only high quality adults adopt. In conclusion, this study uncovered a very interesting complexity underlying an apparently erroneous behavior in the parental care system of avocets. The findings contribute to an understanding of the evolution of the different forms of parental care and throw light on the possible evolutionary mechanisms that led to the current diversity of reproductive strategies in birds.

5.4. TABLES

Table 1. The frequency of adoption in broods of different sizes. Parents with broods of two or three chicks were more likely to adopt than parents with one chick or parents with broods of four (n = 61 broods) or more chicks (n = 9) (G = 8.087, df = 3, p = 0.0443).

Number of resident chicks	**One**	**Two**	**Three**	**Four or more**	**Total**
Number of adopting broods	4	12	25	12	53
Number of non-adopting broods	24	30	47	58	159
Percentage of broods adopting	14.3	28.6	34.7	17.1	25.0
(Total)	(28)	(42)	(72)	(70)	(212)

Table 2. Fate of chicks adopted in various locations and during the three years of the study. Unforced adoptees were those that had left their natal brood before the natal brood departed the nesting island, whereas forced adoptees were those that had been either left behind by their natal brood or whose siblings had died and were abandoned by their parents. Adoption events indicated as "In colony / during brood movement" most likely occurred in the nesting colony but the exact location could not be confirmed. In analyses of chick fledging success, these chicks (n = 20) were combined with chicks adopted in the nesting colony (n = 59).

Location of adoption event	**Motivation of adopted chick**		**Fledged**	**Died**	**Unknown**	**Total**
Nesting colony	Unforced	First-hatched	5	17	0	22
		Second or third-hatched	5	9	0	14
	Forced	Left behind	5	9	0	14
		Siblings died	0	3	0	3
	Unknown		0	5	1	6
In colony / during brood movement	Unforced	First-, second- or third-hatched	3	7	0	10
	Forced	Left behind	3	4	0	7
	Unknown		0	2	1	3
During brood movement	Unforced		0	2	0	2
	Forced	Siblings died	4	2	0	6
	Unknown		2	0	0	2
Feeding areas	Unforced		1	1	0	2
	Forced	Siblings died	1	0	0	1
		Totals	29	61	2	92

5.5. FIGURE LEGENDS AND FIGURES

Figure 1. Mean (± S.E.) number of young fledged per brood as a function of brood size. Both adopted chicks and resident chicks were included in this analysis. Sample sizes (number of broods) are in parentheses. More young fledged from larger broods than from smaller broods (Kruskal-Wallis H = 21.501, df = 4, p = 0.0003).

Figure 2. Mean (± S.E.) prey density on territories of adopting, non-adopting and donor pairs. Prey density was quantified by the residuals of a one-way ANOVA in which year was the main effect and the log-transformed number of aquatic macroscopic invertebrates per liter water was the response variable. The difference between adopting and non-adopting pairs was significant ($F_{2,60} = 4.489$, $p = 0.0152$, Tukey-Kramer $q = 0.359$, $q_{critical} = 0.288$, $p < 0.05$).

Figure 3. Mean (± S.E.) number of young fledged per brood by the adoption status of parents and by brood size. Only resident chicks (the parents' own young) were considered in this analysis. Numbers above bars are sample sizes (number of broods). Both adoption status and brood size influenced the number of young fledged (two-way ANOVA, adoption status: $F_{2,225} = 3.835$, $p = 0.0230$, brood size: $F_{4,225} = 2.714$, $p = 0.0308$, interaction: $F_{4,225} = 0.744$, $p = 0.5629$).

Figure 4. The relationship between prey density on the territory and size of the brood. Prey density was quantified by the residuals of a one-way ANOVA in which year was the main effect and the log-transformed number of aquatic macroscopic invertebrates per liter water was the response variable. $r = 0.355$, $n = 63$, $p = 0.0040$.

Figure 5. Mean (± S.E.) number of chicks in broods used in the clutch manipulation experiment at the time of the broods' departure from the nesting island and at fledging. Experimental clutches were enlarged by adding one or two eggs, whereas controls were not manipulated. Sample sizes are indicated above the bars. Brood size at departure from nesting island differed between treatment levels (Mann-Whitney $U = 1613.5$, $p = 0.0015$), whereas there was no difference in the number of fledglings ($t = 0.564$, df = 125, $p = 0.5740$, naturally adopted chicks were excluded).

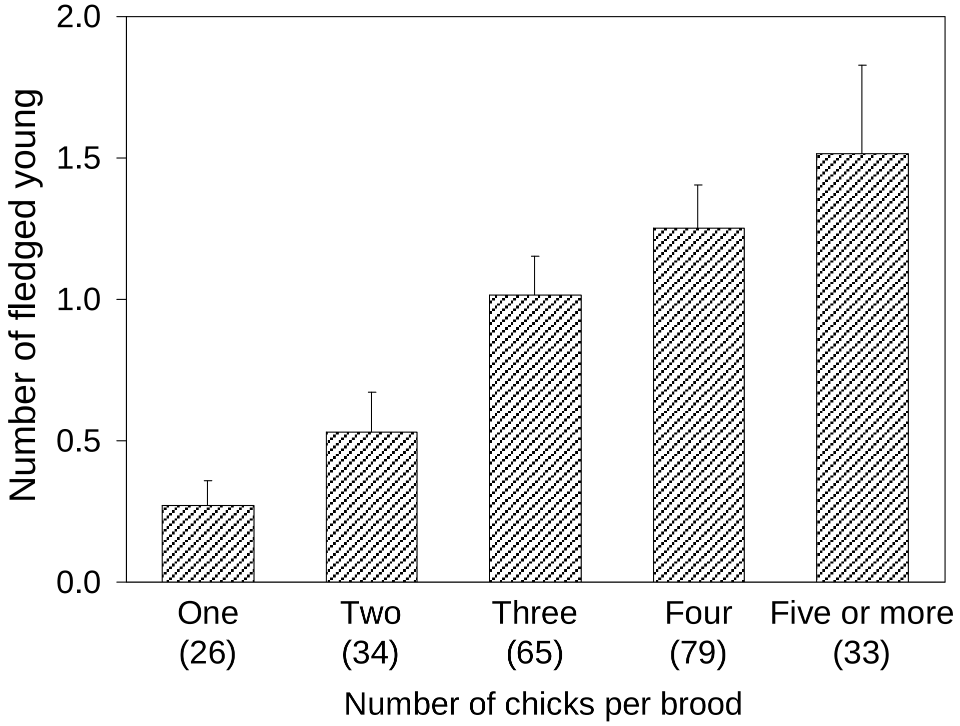
Figure 6. Mean (± S.E.) prey density on territories occupied by pairs with enlarged and control clutches. Prey density was quantified by the residuals of a one-way ANOVA in which year was the main effect and the log-transformed number of aquatic macroscopic invertebrates per liter water was the response variable. Sample sizes are in parentheses. The difference shown was significant (Mann-Whitney $U = 143.0$, $p = 0.0376$).

Figure 7. Mean (± S.E.) percentage of time adults with broods from enlarged and control clutches spent feeding during 30-minute behavioral observations. Sample sizes are in parentheses. The difference shown was significant (Mann-Whitney $U = 11.0$, $p = 0.0394$).

Figure 8. Mean (± S.E.) number of fledged young per brood by brood manipulation treatment level in artificial habitats (A) and natural habitats (B). Sample sizes (number of broods) are given above bars. The difference among treatment levels was significant in artificial

habitats when the effect of brood size was controlled for (treatment $F_{2,51} = 3.621$, $p = 0.0339$; brood size $F_{1,51} = 11.589$, $p = 0.0013$; interaction $F_{2,51} = 2.458$, $p = 0.0957$). Non-independent contrasts showed that broods that had been enlarged fledged more chicks than broods that were not enlarged (modified and control broods combined) ($F = 7.627$, $df = 1$, $p = 0.0080$, $\alpha_{adjusted} = 0.0253$), whereas broods containing experimentally adopted chicks (enlarged and modified broods combined) did not fledge more young than did controls ($F = 3.003$, $df = 1$, $p = 0.0891$, $\alpha_{adjusted} = 0.0253$). There was no difference in the number of fledged young among treatment levels in natural habitats (low predation sites) (**Figure 1.B**, treatment $F_{2,13} = 0.811$, $p = 0.4656$; brood size $F_{1,13} = 0.449$, $p = 0.5147$; $F_{2,13} = 1.548$, $p = 0.2494$).

Chapter 5, Figure 1.



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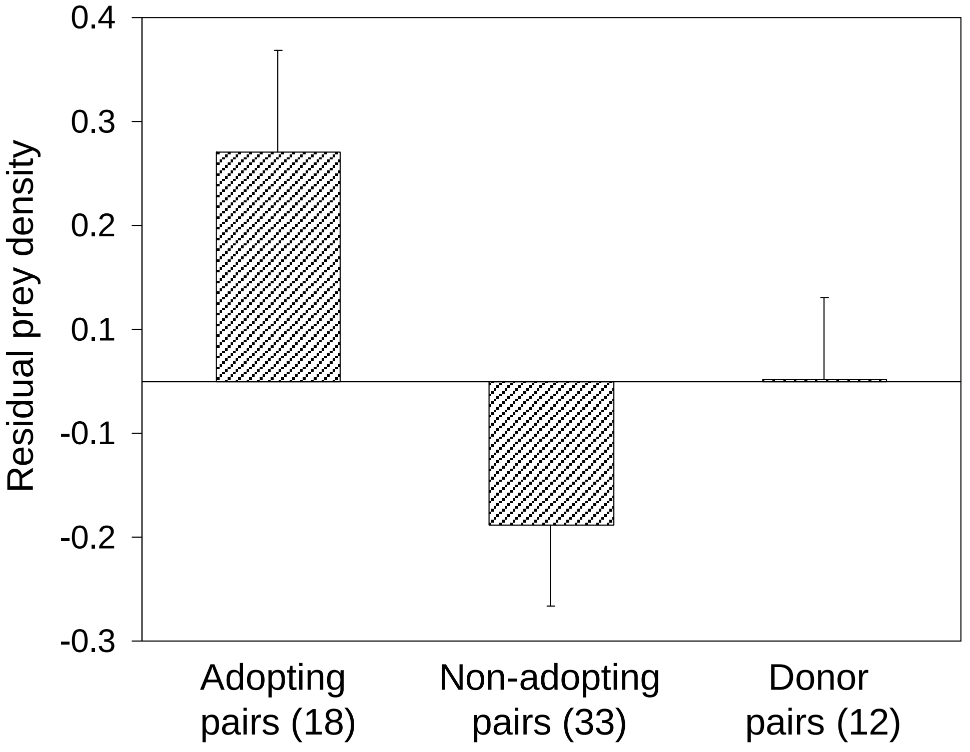

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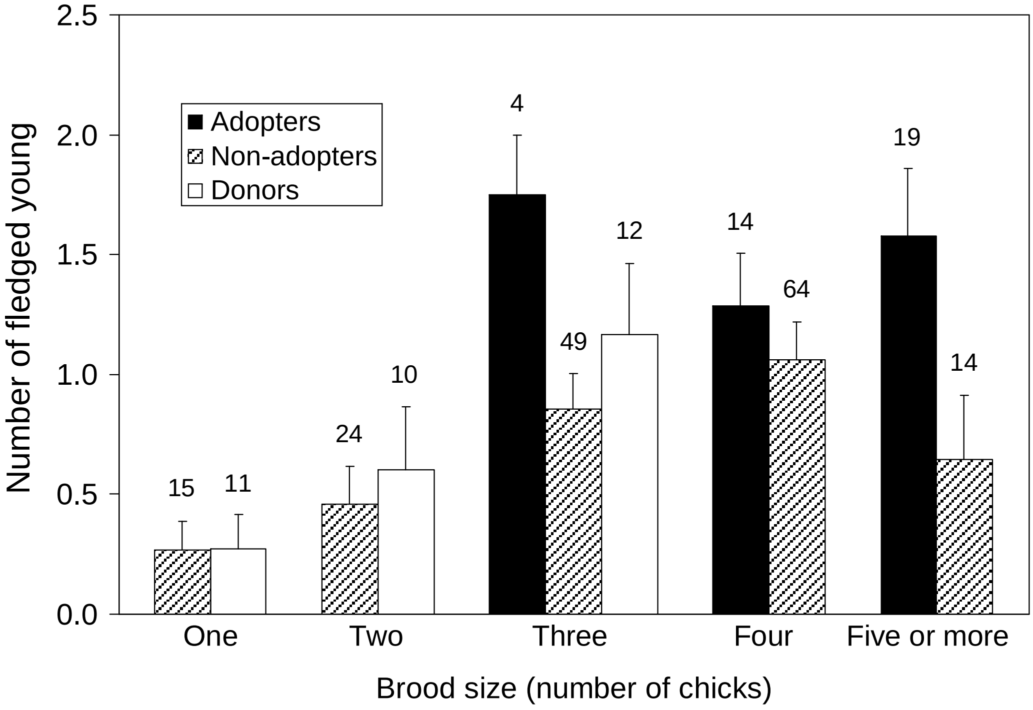

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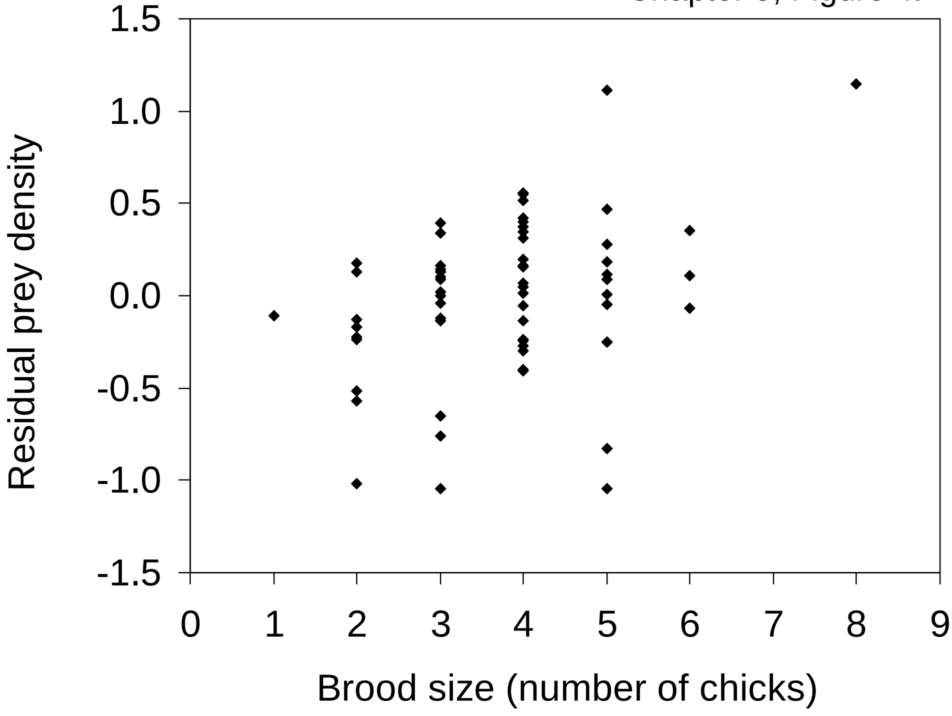

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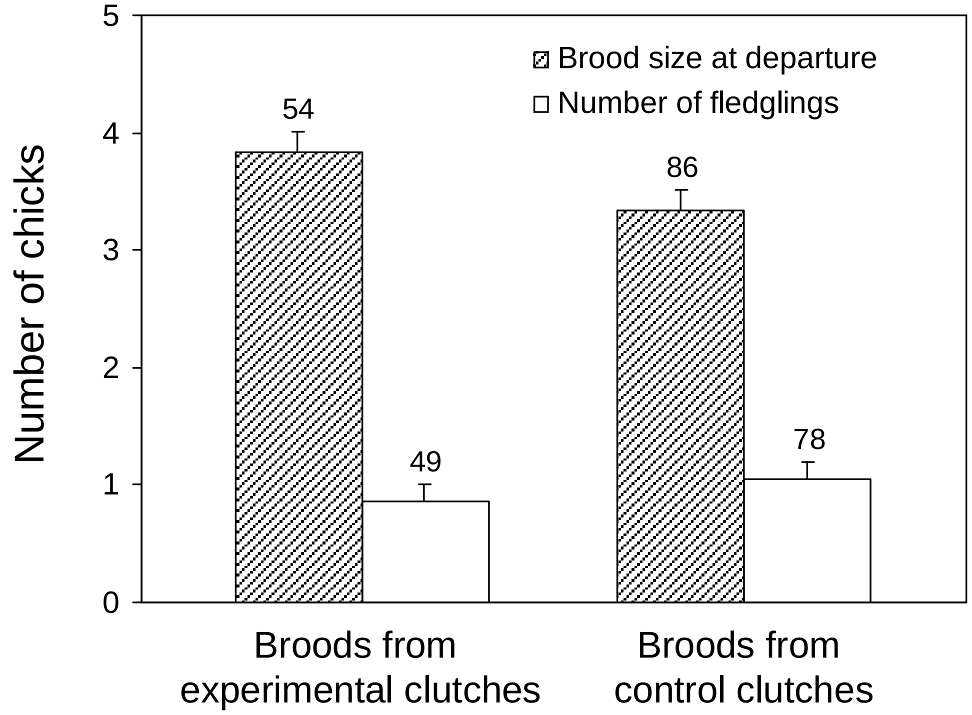

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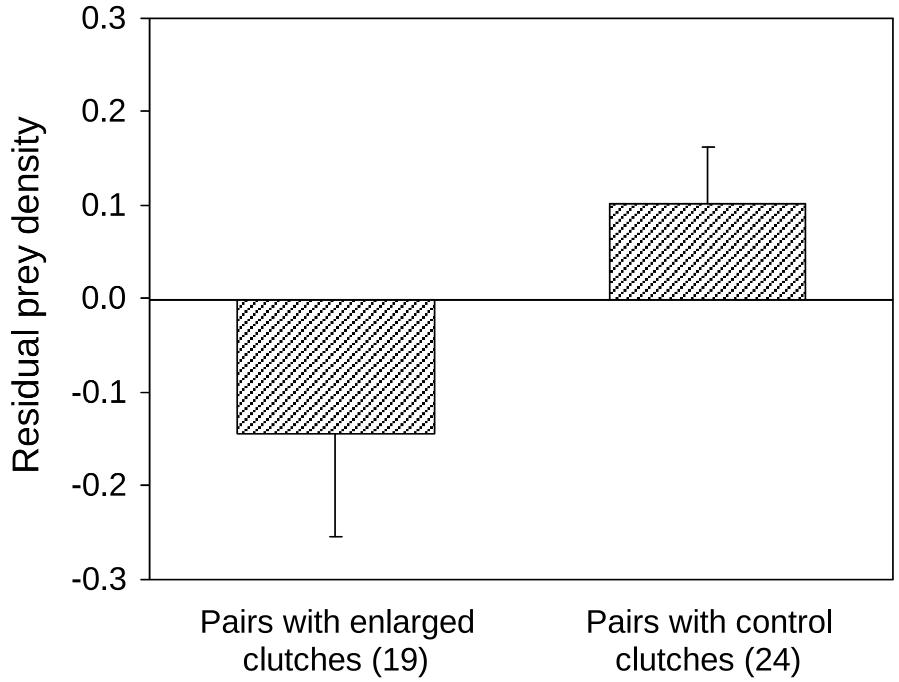

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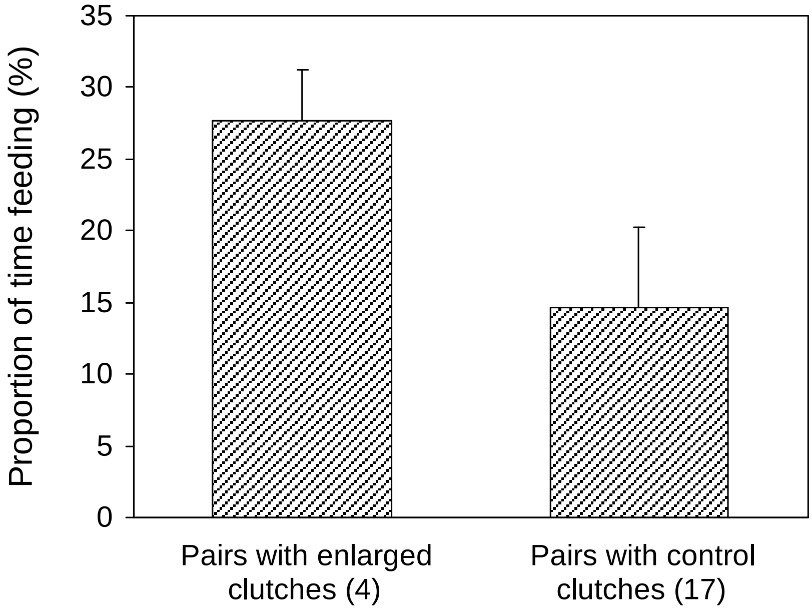

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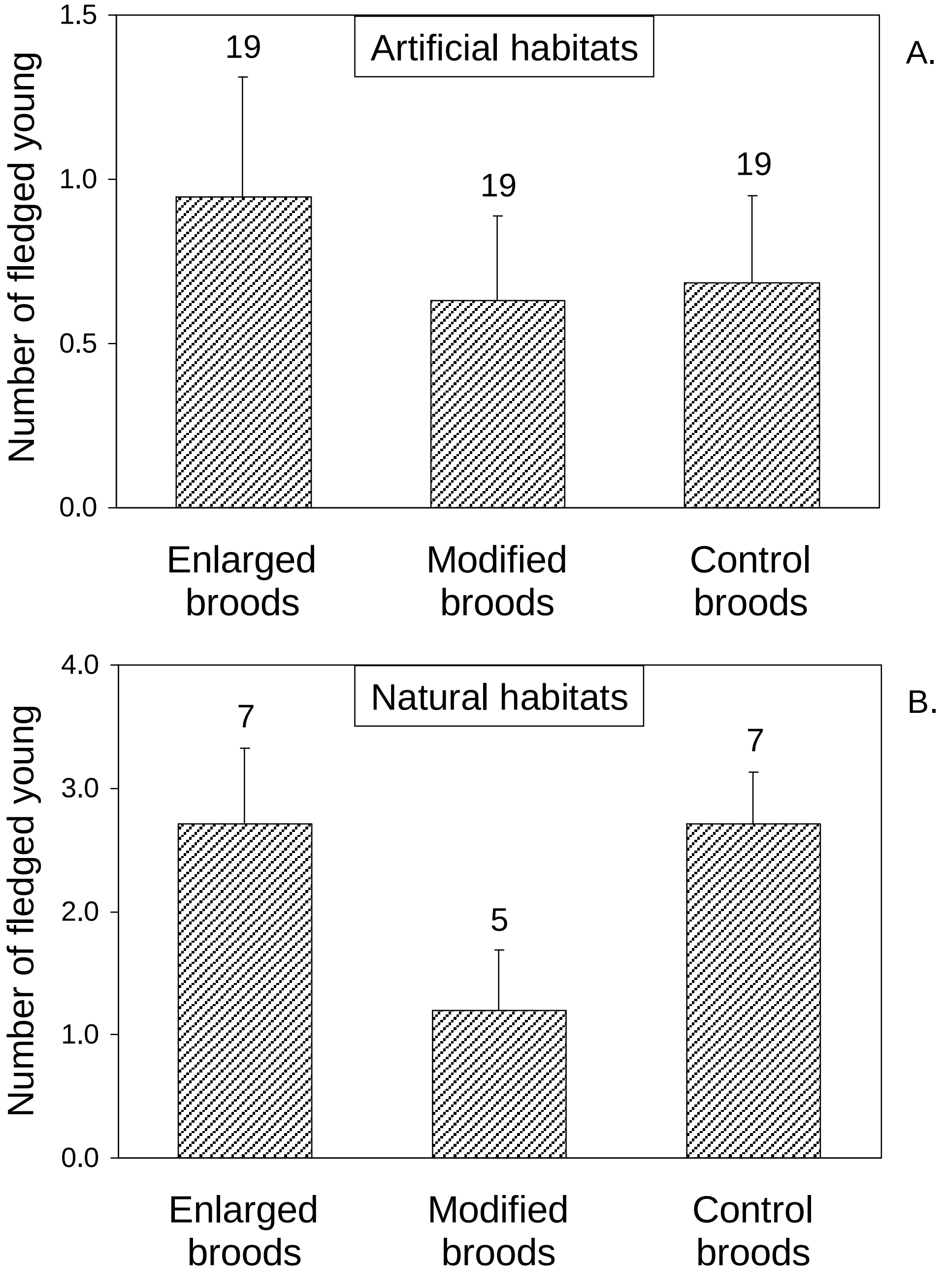

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