



Feeding constraints and parental care in female eiders

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Academic dissertation

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- I** Hario, M. & Öst, M.: The effect of local food resources on feeding and breeding performance of a migrant capital breeder, the eider *Somateria mollissima*. – Submitted.
- II** Öst, M. 1999: Within-season and between-year variation in the structure of common eider broods. – *Condor* 101: 598–606.
- III** Öst, M. & Kilpi, M. 1999: Parental care influences the feeding behaviour of female eiders *Somateria mollissima*. – *Annales Zoologici Fennici* 36: 195–204.
- IV** Öst, M. & Kilpi, M. 2000: Eider females and broods from neighboring colonies use segregated local feeding areas. – *Waterbirds*, in press.
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Study design and methods	MÖ, MH	MÖ, MK	MÖ, MK	MÖ, MK	MÖ, MK, KL
Data gathering	MÖ, MH, MK, JTL, OM, MW	MÖ	MÖ	MÖ, MK, MW	MÖ, MK, MW
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Introduction

Life-history strategies are the ways in which organisms acquire and expend resources on different organism functions such as maintenance, growth and reproduction. Because these functions compete for the same limited resource pool, trade-offs between life history traits are to be expected (Levins 1968). Perhaps the most fundamental life-history trade-off is the cost of reproduction (*sensu* Williams 1966, Charnov & Krebs 1974); current reproduction carries a cost in terms of either future survival or future reproduction (reviewed in, e.g., Lindén & Møller 1989, Stearns 1989, 1992, Dijkstra et al. 1990, Clutton-Brock 1991, Lessells 1991, Roff 1992). If the costs of reproduction become too high relative to the benefits, this may lead to situations where it no longer pays for a parent to continue investment in current reproduction. However, a parent may still have the choice of salvaging some reproductive success if it succeeds in donating its offspring to the care of conspecifics. This is the rationale of the salvage strategy hypothesis for brood abandonment (e.g., Lack 1968, Eadie et al. 1988). The parent would in this case be “making the best of a bad situation”, i.e. a type of conditional evolutionary stable strategy (*sensu* Maynard Smith & Price 1973).

Feeding activity patterns determine the amount of energy acquired and thereby connect physiological ecology and life history evolution (Stearns 1992). Probably all organisms reproduce by at least partially compensating for the extra energy needed during reproduction (e.g., Tuomi et al. 1983, Jönsson 1997). The timing of resource compensation has important life history consequences. There are two different tactics of resource compensation. “Income breeders” increase their feeding rate while reproducing and do not rely on energy stores, whereas “capital breeders” rely upon energy gathered at some previous time, and stored until later use (Drent & Daan 1980). The capital and income dichotomy describes a continuum of provisioning strategies ranging from immediate use to long-term storage (Thomas 1988,

Stearns 1992, Bonnet et al. 1998, Meijer & Drent 1999). Current and future reproduction are linked in capital breeders through the shared energy store and we may expect to find trade-offs between current and future reproduction (Stearns 1992). In income breeders, high metabolic rates rapidly eliminate the physiological traces of reproduction and we may fail to find the trade-offs expected.

Why would individuals other than the genetic parents raise conspecific offspring? Alloparental care (*sensu* Wilson 1975) intuitively seems inconsistent with classic evolutionary theory, because its occurrence apparently violates the Darwinian principle by which animals are selected not to expend resources in the propagation of competing genotypes. Nevertheless it occurs in a variety of organisms, including fishes (e.g., Wisendon & Keenleyside 1992), insects (e.g., Sherman et al. 1995), annelids (Premoli & Sella 1995), mammals (reviewed in Riedman 1982), and birds (reviewed in Brown 1987, Eadie et al. 1988). Despite the widespread occurrence of alloparental care in diverse taxonomic groups, it is still unclear why parents accept and care for young that are not their own. Descriptions of alloparental care in birds have generally involved nonbreeding adults helping at the nest or breeding adults raising young in communal nests (e.g., Riedman 1982, Brown 1987, Emlen & Wrege 1989). By comparison, crèching behaviour, or brood amalgamation – young from different broods/families combine into a single group and subsequently receive care from parents other than their own – has so far received less attention (Eadie et al. 1988, Lanctot et al. 1995). Crèching is particularly common among waterfowl (Eadie et al. 1988, Beauchamp 1997, 1998b), but has often been omitted from major reviews of co-operative breeding (e.g., Riedman 1982, Brown 1987). One reason for this neglect may be that the association of waterfowl young with other than their genetic parents has been regarded as accidental, facilitated by various disturbances, and thus of no adaptive value (e.g., Patterson 1982, Savard 1982, Savard et al. 1998). There has recently been a heated discussion about the proximate

and ultimate causes of brood abandonment and adoption also among the advocates of adaptive explanations of crèching behaviour (Bustnes & Erikstad 1995, Pöysä 1995, Pöysä et al. 1997, Eadie & Lyon 1998, Pöysä & Milonoff 1999). However, because the variation in crèching behaviour among waterfowl is considerable (**II**), we should refrain from drawing too far-reaching conclusions about its function for the whole group based on observations of only single species (Eadie & Lyon 1998). The determinants of intra-specific brood amalgamation in waterfowl remain poorly understood (Beauchamp 1997), and a lot of work awaits us.

Waterfowl exhibit considerable inter-specific variation in life history traits and this has caused some confusion and controversy among the researchers in this field. For example, species differ greatly in their reliance on endogenous reserves versus exogenous resources for reproduction (Meijer & Drent 1999), and this variation has probably contributed to the controversy about the factors that limit clutch size in precocial birds (e.g., Ankney et al. 1991, Arnold & Rohwer 1991, Rohwer 1992). Another controversial issue is the relative importance of food intake at the breeding grounds and reserves stored at the wintering quarters in some migrating waterfowl, which conventionally have been classified as pure capital breeders (e.g., Alisauskas & Ankney 1992, Chonière & Gauthier 1995, Ganter & Cooke 1996).

In this thesis (**I–V**), I study the breeding biology and feeding constraints associated with breeding in female eiders (*Somateria mollissima*) nesting in the northern Baltic Sea. Eiders are extreme capital breeders (Korschgen 1977, Parker & Holm 1990, Kilpi & Lindström 1997, Meijer & Drent 1999), and they face high costs of reproduction during egg laying and incubation. The reliance on energy stores creates a physiological link between the pre-hatching and post-hatching periods in the breeding cycle. The richness of the eider's parental care system makes this species especially well suited for the study of processes underlying parental care decisions and crèching behaviour. My main objectives

are twofold: 1) to examine feeding constraints prior to egg laying and incubation, and the relative importance of local food resources for breeding performance, and 2) to study brood-rearing behaviour, thereby trying to identify the key factors responsible for parental care decisions.

Outline of the thesis

The five papers of the thesis cover the breeding cycle of female eiders at their breeding ground in the northern Baltic, from the pre-laying period till the end of brood-rearing. I will follow the same chronological order in the discussion that follows the description of the study system in the summary. In this discussion I will put my main findings into a broader scientific context.

The focus in paper **I** is on the pre-hatching period. I compare the pre-laying foraging behaviour and breeding performance of female eiders nesting at two localities in the Gulf of Finland, which differ greatly with respect to the amount of food available. I explore the effects of local food conditions on feeding prior to laying, and I also assess the relative importance of local food resources and reserves stored prior to arrival as clutch size determining factors. To achieve this aim, I compare between-year variation in food availability, both between and within sites, with variation in female body weights at incubation onset and clutch size.

In paper **II**, I proceed to the post-hatching period. I describe the compositional structure of eider broods in the northern Baltic. The data stem from standardised brood censuses extending over a period of four years, and the focus is on within-season and between-year variation in the structure of broods. The potential role of female aggression and female body condition at hatching in the shaping of these patterns are also discussed.

Paper **III** compares the feeding behaviour of females adopting different parental care modes. I focus on the use of feeding habitat and feeding technique. Females caring for

young may be constrained in their feeding behaviour compared to females freed of parental duties. The first aim was to compare the feeding behaviour of these two categories of females. The second aim was to test a novel hypothesis that the crèche system of eiders, where several females jointly care for young, may allow females flexibility as to feeding method and site, while still participating in brood care.

In paper IV, I compare the habitat use of females adopting different parental care strategies on a larger spatial scale than in paper III. I examine the dispersion pattern and degree of separation of females from neighbouring colonies, and I also discuss which implications the observed dispersion pattern might have for post-hatch brood amalgamation behaviour.

In paper V, I continue on the theme of relating female parental care mode to female characteristics such as body condition, but a more detailed picture of these relationships emerges because females were individually known. The main purpose of the study is to test the validity of the energetic salvage strategy hypothesis for brood abandonment. This paper also gives an indication of the complexity of the eider parental care system; a complexity that has largely been overlooked in studies so far.

The study system

The eider is a widespread and abundant sea duck with a northern Holarctic distribution. Adults in the non-breeding season feed mainly on molluscs and other benthic invertebrates (e.g., Madsen 1954, Beauchamp et al. 1992, Öst & Kilpi 1998), whereas females and young in the breeding season often utilise a different diet consisting of, e.g., crustaceans (reviewed in III). Eiders are extreme capital breeders and they do not eat during laying and incubation (I, Korschgen 1977, Parker & Holm 1990, Kilpi & Lindström 1997). The parental care system of eiders is unique among waterfowl because many females may

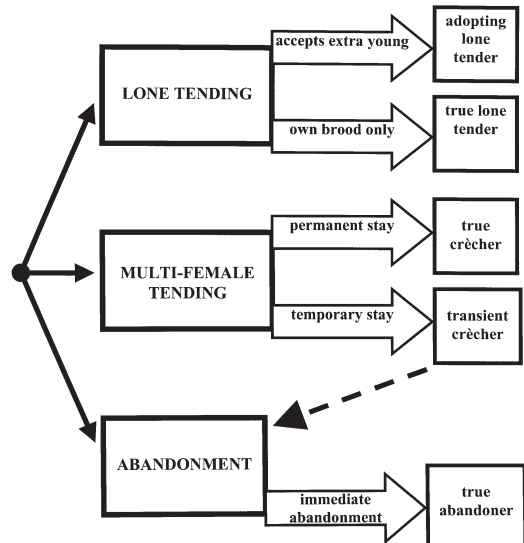
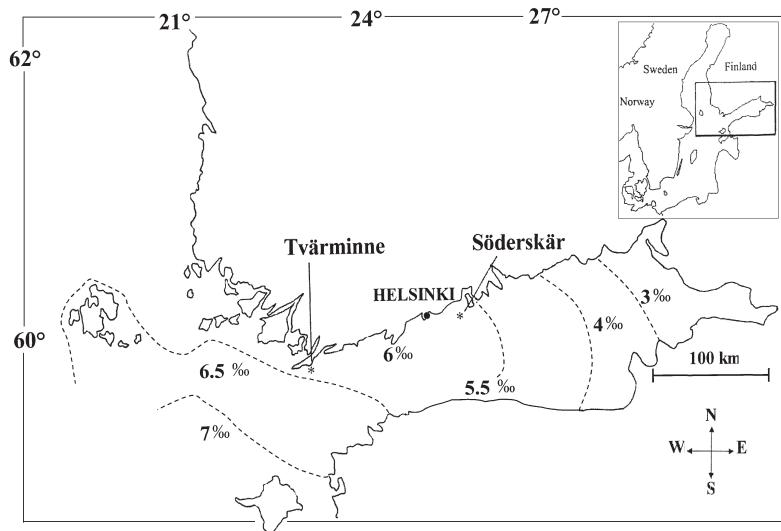


Figure 1. Schematic representation of the parental care strategies used by eider females. Terminology follows the one applied in paper V.

jointly care for young, and this system has been the subject of extensive study (e.g., Gorman & Milne 1972, Bédard & Munro 1976, Munro & Bédard 1977a, 1977b, Schmutz et al. 1982, Bustnes & Erikstad 1991a, 1991b). Females are solely responsible for parental care, and they use three basic parental care modes: (1) care for young by a single female, either caring for her own brood or also accepting unrelated young, (2) joint care by two or more females, which may involve acceptance of unrelated young, and (3) abandonment of young (Fig. 1, II, V). To add to the complexity, multi-female tenders can be further subdivided into “true crèches” permanently staying in the same crèche, and “transient crèches” which initially attend a multi-female brood but soon leave (Fig. 1, V). Eiders are colonial nesters, which certainly offers an advantage for studies in parental care behaviour, because this facilitates capture of large samples of birds.

The eider is the most abundant sea duck in the Baltic (Stjernberg 1982, Hario & Selin 1986), and the eiders breeding in the northern parts of the Baltic migrate from their wintering grounds in the Danish Straits (Alerstam et

Figure 2. Map of the study area. Most of the data were collected at Tvärminne Zoological Station, but some data were also collected at Söderskär Game Research Station. The map also shows the generalised salinity isopleths in the Gulf of Finland and the northern Baltic proper according to Furman (1992).



al. 1974, Noer 1991). The Baltic Sea is brackish and relatively few prey species are available for eiders compared to truly marine habitats (III). Eiders from the northern Baltic feed almost exclusively on blue mussels *Mytilus edulis* in the non-breeding season (e.g., Bagge et al. 1973, Nilsson 1980), whereas small ducklings mainly feed on a few species of amphipods found along the shorelines of islands (V, Hario et al. 1992).

This study was carried out in the northern Baltic, east of Hanko, southwestern Finland, in the archipelago surrounding Tvärminne Zoological Station (59°50'N, 23°15'E) (Fig. 2). In addition, part of the data in paper I were collected at Söderskär Game Research Station (60°07'N, 25°25'E), in the central Gulf of Finland (Fig. 2). The Tvärminne study area can be described as a complex of islands, islets, and small skerries. Eiders breed on small, open islands and on larger, wooded islands. This division of breeding areas into open and wooded habitat has important consequences for female incubation costs; females breeding in open habitat face higher costs, and this in turn influences their clutch size (Kilpi & Lindström 1997). The eider colonies around Tvärminne are all relatively small (less than 150 nests per island) and located close to each other (IV). Söderskär is an island group of about 25 mainly treeless islets in the outer ar-

chipelago. The eider population at Tvärminne has been fairly stable at roughly 1,500 pairs during the last decade, whereas the Söderskär population has declined c. 60% from 2,300 pairs in the mid 1980s to only 950 pairs in 1999.

The pre-hatching period

Effect of local food resources on feeding prior to laying

There has been a recent upsurge of studies dealing with the fitness consequences of environmental degradation on waterfowl. Deteriorating food conditions may affect fecundity (e.g., Cooch et al. 1989, Coulson 1999), growth, body size and survival of ducklings (e.g., Cooch et al. 1991, 1993, Williams et al. 1993, Coulson 1999), as well as the final adult size (Larsson & Forslund 1991, Larsson et al. 1998). Blue mussels, the staple food of eiders, have declined in both size and numbers throughout the Gulf of Finland since the late 1970s (Öst & Kilpi 1997). To explore the effect of local food resources on breeding eider females, their pre-laying foraging behaviour and breeding performance were compared at Tvärminne and Söderskär, situated at oppo-

site ends of a blue mussel gradient running in east–west direction through the Gulf of Finland (Fig. 2, **I**). As expected, the densities and biomass of blue mussels of preferable size for eiders (Öst & Kilpi 1998) were higher at Tvärminne (**I**). The length of female foraging cycles and the time devoted to active feeding were considerably greater at Söderskär with less available food. Females from Söderskär probably must feed longer to obtain the food equivalent to a meal (Guillemette et al. 1992), indicating a greater pre-laying foraging effort. These results are consistent with those of Vickery et al. (1995) – as a result of food depletion, brent geese *Branta bernicla* fed more intensively and for a greater percentage of time, yet the net result was a declining intake rate. Likewise, Gloutney et al. (1999) found that snow geese (*Anser c. caerulescens*) and Ross's geese (*A. rossii*) foraged for more than 7.6 h per day at the breeding colony, but obtained less than 1.4 g forage (dry mass) per hour while foraging.

Can food at the breeding grounds influence fecundity?

According to Lack (1967, 1968), food available to the laying female limit clutch size in precocial birds, although this hypothesis has later been severely criticised (e.g., Arnold & Rohwer 1991, Rohwer 1992). However, the consensus is that clutch size in Arctic-nesting geese and eiders subject to breeding anorexia is limited by endogenous nutrient reserves (reviewed in Rohwer 1992), albeit the importance of dietary food intake has probably been underestimated in geese (Meijer & Drent 1999). Lack's hypothesis was later modified by Ryder (1970), who proposed that clutch size in Arctic-nesting geese is determined by the amount of female body reserves on arrival. The influential paper by Ankney & MacInnes (1978) supported this notion by showing that heavier arriving female geese had, on average, larger potential clutches (i.e. more developing follicles). Ryder's hypothesis implicitly assumes that the pre-laying period spent at the breeding grounds is energeti-

cally costly to females. However, there is now convincing evidence that this assumption has been prematurely accepted, at least in geese – extensive pre-nesting feeding does occur at the breeding grounds, this period can be energetically beneficial, and thus local food condition may have an impact on clutch size (e.g., Parker & Holm 1990, Budeau et al. 1991, Bromley & Jarvis 1993, Choinière & Gauthier 1995, Ganther & Cooke 1996).

Eiders breeding at Tvärminne and Söderskär winter in the Danish Straits, and the spring passage through the Swedish east coast is fairly rapid and synchronised (Alerstam et al. 1974). According to my results (**I**), food at the breeding grounds is predominantly for maintenance, and for deferring the use of reserves acquired before arrival. Furthermore, local food conditions appeared to have little impact on clutch size. I base these conclusions on the following findings; (i) clutch size and female body weight at incubation were similar at Tvärminne and Söderskär, though the pre-laying foraging behaviour was markedly different, (ii) pre-laying foraging behaviour was similar among years at Söderskär despite significant annual variation in clutch size and body weights, (iii) the between-year variation in clutch size and body weights at incubation onset showed slight parallelism between localities, and (iv) the between-year variation in food availability within study sites seemed unrelated to female pre-laying foraging behaviour, clutch size, or body weight at incubation onset (**I**). As a paradoxical example, average female body weight at incubation onset at Söderskär was lowest in the year when the biomass of food was the highest (**I**). Hence accumulation of sufficient body reserves before arrival may be a prerequisite for successful breeding in the northern Baltic, at least in the existing circumstances. In contrast, environmental degradation may lead to a systematic long-term decline in clutch size in a sedentary eider population (Coulson 1999).

The recent population decrease of eiders in the central and eastern parts of the Gulf of Finland (Hario et al. 1992) may therefore be attributable to other demographic traits than

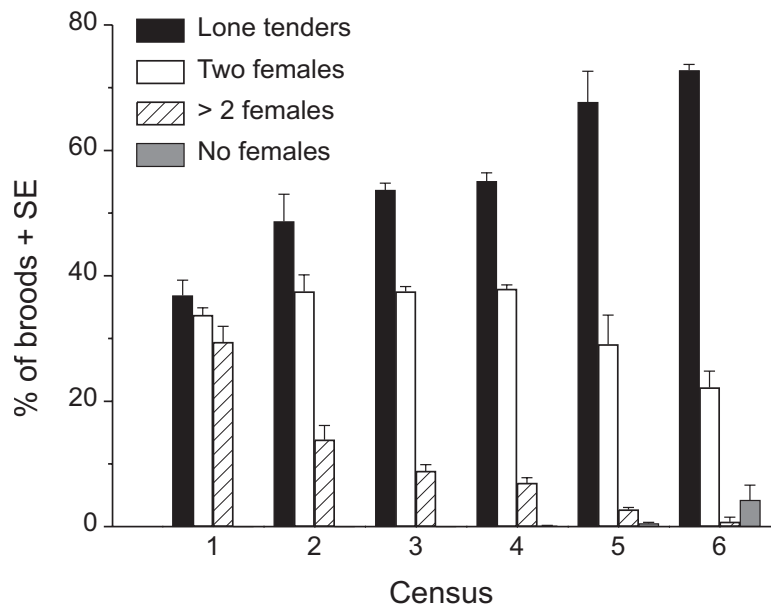
clutch size. One alternative explanation is lowered juvenile survival (I). Fledgling production at Söderskär has indeed been highly variable and low for the last decade and, consequently, recruitment to the breeding population has been insufficient to compensate for adult mortality (Hario & Selin in press). Fledgling production has also been variable at Tvärminne, but generally higher than at Söderskär (II). Local food conditions may thus affect juvenile survival, although the relative contribution of pathogens to mortality and their interaction with food shortage remains obscure (Hollmén et al. 1996, 1999). Also according to J. C. Coulson (pers. comm.), duckling survival appears to be the key to understanding the population dynamics of eiders. Regardless of the reasons for the negative trend in population size, the high natal and breeding philopatry of eider females at Söderskär (Tiedemann & Noer 1998, Tiedemann et al. 1999) currently appears maladaptive. That philopatric behaviours may become maladaptive in a population under conditions of systematic deterioration of feeding areas, has also been demonstrated in lesser snow geese (Cooch et al. 1993, Rockwell et al. 1993, Williams et al. 1993) and western gulls (*Larus occidentalis*) (Spear et al. 1998).

The post-hatching period

Frequencies of eider care modes

I found that the structure of eider broods at Tvärminne showed a regular pattern of within-season change (Fig. 3, II), and a distinct pattern of between-year variation (Fig. 4, II). On the whole, multi-female tending (tantamount to crèching in V) was the prevalent care mode initially, i.e. soon after broods had hatched and reached the water (Fig. 3, II, Table 2 in V). Brood abandoning females usually made up the secondmost frequent group of females (Table 2 in V), followed by lone tenders (Fig. 3, II, Table 2 in V). The number of females in broods was most variable around peak hatching, but broods with more than two attending females decreased to a low level within two weeks (Fig. 3, II). Lone tenders, on the other hand, increased in frequency throughout the breeding season, and the frequency of two-female broods was fairly stable throughout the season (Fig. 3, II). These patterns may well be a consequence of females termed “transient crèchers” leaving the broods, usually within one week after the brood had reached the water (V). Possible mechanisms underlying this behaviour are

Figure 3. Within-season change in the structure of eider broods. The proportion of broods tended by lone tenders, two females, more than two females, and broods without tending females in the censuses 1995–1999. The proportions shown are annual averages. Censuses 1 and 2 were conducted in all 5 years, census 5 in all years except 1996, censuses 3 and 4 in 3 years (1997–1999) and census 6 in 2 years (1997–1998) (see also II).



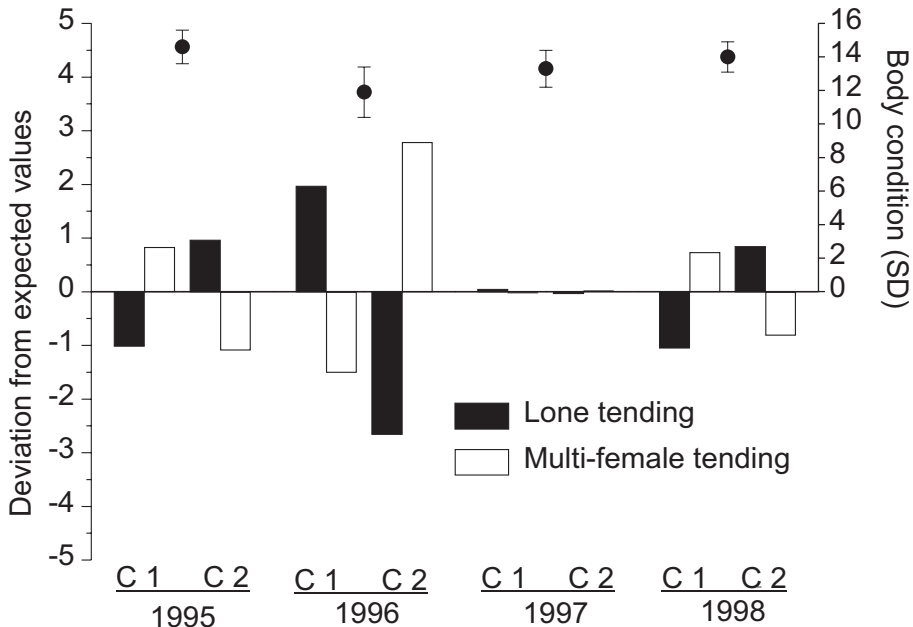


Figure 4. Between-year variation in the structure of eider broods. Deviations between observed and expected frequencies of lone tenders and multi-female broods in the first two censuses in 1995–1998 (C 1 = census 1, C 2 = census 2). These deviations are described by the standardised residuals of a log-linear model described in II. The dots show the mean body condition index (weight at hatching/radius-ulna length) \pm SD of females in 1995–1998. The condition index was significantly higher in 1995 and 1998 than in 1997, and the index was lowest in 1996 (II).

detailed in the remaining discussion. In addition, two-female broods seem to decrease slightly in frequency when family units start to disintegrate later in the breeding season, which may further increase the proportion of lone tenders (Fig. 3, II).

Apart from the variable phase immediately following hatch that coincides with the departure of transient crèchers, brood composition in my study area appears stable (II, V). The number of females in broods was roughly the same during the 2–7 weeks posthatch, indirectly indicating stability (II). Average observation times of marked females adopting different parental care modes were close to 30 days, confirming the duration of female attendance in crèches once formed (V). These values of stability are probably underestimates, either because we lost track of the broods, or the females lost their coloured flags used as

temporary individual markers. Crèche stability is of similar duration in the St Lawrence estuary in Canada, the minimum duration of the parental bond being 40 days (Bédard & Munro 1976). The structure of eider broods at the Ythan estuary in Scotland seems exceptional in this respect: Gorman & Milne (1972) found that crèches were attended by a constantly rotating cohort of females, each female remaining, on average, only four days with the young. This instability might result from the large-scale spatial segregation between duckling and adult foods (Gorman & Milne 1972, Swennen 1989), which according to Gorman & Milne (1972) forces females to leave the young in order to feed.

Multi-female broods were initially more common in years when females were in good condition at hatching and less common in years when females were in poor condition

(Fig. 4, **II**). However, multi-female broods decreased in frequency over time in all years except the poorest year, and, within two weeks, the multi-female tending strategy was proportionally most common in poor years and least common in good years (Fig. 4, **II**). Besides being related to average female body condition, these between-year patterns in the frequencies of tending strategies might also be caused by, for example, annual variation in brood mortality. Such a causal relationship could arise if females base their decision to abandon on the mortality rate of the brood (the “brood success hypothesis”; e.g., Pöysä et al. 1997). There are some indirect indications, however, that female body condition *per se* may have a stronger influence on these between-year patterns. Females were in good condition at hatching in 1998, yet duckling mortality was almost as high as in the poor year 1996 when both female condition at hatching and duckling survival were poor. The frequencies of lone tenders and multi-female tenders in the first two censuses closely resemble those of the best year 1995, when average female condition was the highest (Fig. 4, **II**). How exactly body condition relates to tending strategies remains unclear, however. Whereas a preliminary analysis of a smaller data set suggested that lone tenders had a slightly, but not significantly, poorer body condition than multi-female tenders (**II**), augmentation of the data revealed no significant differences in body condition between the groups; in fact, this analysis singled out lone tenders as having the highest mean condition index (**V**). For a discussion about body condition and other factors possibly inducing between-year variation in tending strategies, I refer the reader to the chapter dealing with open questions.

Habitat use

Breeding status appeared to have only a minor impact on female post-nesting site use and movements at large (**IV**). Female primary movements (for definition, see **IV**) and home range were similar among lone tenders,

multi-female tenders, and failed nesters without young. Female secondary movements (for definition, see **IV**) tended to be shorter among lone tenders than among females without young (**IV**). These results are in accordance with Bustnes (1996), who found that parental care did not constrain habitat use much, but that females without young undertook longer secondary movements. However, if we study the habitat use of caring and non-caring females on a finer spatial scale, a very different picture emerges: parental care clearly constrains female habitat use, feeding technique, and diet (**III**). Females tending small young feed like their young, mainly on gammarids (*Gammarus* spp.) found close to the shore, whereas non-tending females feed on mussels found slightly farther out from shore (**III**).

I found some indications that food resources may influence female post-nesting site use. Blue mussels are more abundant further out at sea at Tvärminne, and, correspondingly, the home ranges of females from colonies in the outer study area were significantly smaller than those of females from the innermost colony (**IV**). Home range size was also positively correlated with the number of ducklings in broods (**IV**), suggesting that larger broods need more food and also a larger feeding area (cf. Håland 1983, Gauthier 1987a). Hence it may seem surprising that home ranges were similar in size irrespective of female breeding status, given that multi-female broods, on the average, contained more ducklings than broods tended by single females (**IV**). One possible explanation might be that broods with more tending females may possess a higher dominance rank, allowing these broods to compete more successfully for limited food resources (see Emlen & Wrege 1989, Emlen et al. 1991, Williams 1994, Nastase & Sherry 1997). Social dominance is associated with group size in many waterfowl, larger family units dominating over smaller (e.g., Black & Owen 1989, Gregoire & Ankney 1990, Williams 1994, Lepage et al. 1998, Loonen et al. 1999). The home range size of lone tenders tended to vary more (**IV**), which may imply that a part

of these broods may have been compelled to use a larger feeding area.

The habitat use of waterfowl during the rearing season has received relatively little attention (Anderson & Titman 1992, Nummi & Pöysä 1995). While swans and ducks show vigorous defence of nesting territories, ducks are usually less territorial (Håland 1983, Gauthier 1987a), with a few exceptions such as shelducks and goldeneyes (Patterson 1982, Savard 1982, Gauthier 1987a, Afton & Paulus 1992). Eiders are gregarious during the brood-rearing season (Ahlén & Andersson 1970, Gorman & Milne 1972, Minot 1980), and therefore they are not expected to monopolise post-nesting feeding and loafing sites (Bustnes & Erikstad 1991a). Eider broods in many areas typically conduct a long-distance nest exodus from the breeding colony to the rearing areas in the first few days after hatch (Ahlén & Andersson 1970, Bédard & Munro 1976, Minot 1980, Sedinger 1992, Bustnes & Erikstad 1993).

Eider females and broods at Tvärminne did not conduct a long-distance nest exodus after hatch; they settled close (usually less than 1 km) to their nesting island (IV). This is obviously because shallow areas with suitable feeding patches for small ducklings surround many of the islands in the study area. I also found that females and broods from the same colony were significantly aggregated to the same site close to their colony, whereas females and broods from neighbouring colonies – in spite of the colonies being geographically located very close to each other – were essentially spatially separated (IV). That females and broods from the same colony congregated at the same post-nesting feeding site may simply reflect that they moved to the nearest available feeding site. The benefits of familiarity with available food resources may be enhanced during brood-rearing (Bustnes & Erikstad 1993, Lindberg & Sedinger 1997), although direct evidence for advantages of site familiarity is hard to come by (Hepp et al. 1989, Anderson et al. 1992, Hepp & Kennamer 1992, Lindberg & Sedinger 1997). Moreover, aggregation of colony members may be promoted by conspecific attraction;

attraction towards feeding conspecifics is common for social foragers as it may enable increased feeding efficiency (reviewed in, e.g., Pöysä 1992, Beauchamp et al. 1997). On the contrary, the spatial segregation of birds from neighbouring colonies seems surprising considering that female waterfowl are assumed to roam widely during brood-rearing (Anderson & Titman 1992).

Besides being a consequence of broods moving to the nearest available feeding site (which by no means all broods do; the longest recorded movement distances from the nesting site to the first observation of brood-caring females were 4 km), this dispersion pattern may also result from agonistic interactions or mutual avoidance among females from different colonies (IV). The food of small ducklings is spatially restricted to the shorelines of islands that cover only a limited area (III, Hario et al. 1992), so there would potentially be scope for competition and monopolisation of these resources – spatial clumping of food increases its monopolisation and defence (e.g., Grant & Guha 1993, Beauchamp 1998a).

Because post-hatch brood amalgamation usually occurs soon after the brood has left the nest (V), at the rearing sites, females in multi-female broods may originate from the same island (IV). This may have important consequences. Eider females show strong natal and breeding philopatry (Swennen 1976, 1990, Coulson 1984, Baillie & Milne 1989, Bustnes & Erikstad 1993), leading to a very low gene flow among eider colonies (Tiedemann & Noer 1998, Tiedemann et al. 1999). Eider colonies might therefore largely consist of related females (Tiedemann & Noer 1998), so kin selection (Hamilton 1964) could be important in post-hatch brood amalgamation. Alternatively, because eiders are long-lived (Coulson 1999), individual recognition may be prevalent in waterfowl (cf. Savard 1985, Gauthier 1987b), and females repeatedly encounter the same individuals in consecutive seasons, reciprocity could also drive post-hatch brood amalgamation behaviour (see Eadie et al. 1988, Emlen & Wrege 1989, Emlen et al. 1991).

Post-hatch brood amalgamation

Eadie et al. (1988) were the first to compile the hypotheses that have been proposed to explain pre-hatch and post-hatch brood amalgamation and to present a theoretical framework for the evolution of these behaviours, thereby paving the way for explicit testing among competing alternative hypotheses. In what follows, I will present the hypotheses proposed to explain post-hatch brood amalgamation using the theoretical framework erected by Eadie et al. (1988), adding some hypotheses that were missing from their original formulation. I will also discuss the evidence supporting or refuting these hypotheses, in the light of my own findings as well as those of others. Finally, I will present a synopsis of the most plausible explanations of post-hatch brood amalgamation in eiders as well as other waterfowl.

Why be a donor of young?

Accidental brood mixing hypothesis

Post-hatch brood amalgamation in waterfowl has been regarded as a nonselected consequence of accidental brood mixing before strong bonds between mother and young develop (e.g., Munro & Bédard 1977a, 1977b, Afton 1993). Brood mixing may be enhanced by predation (Munro & Bédard 1977a, 1977b) or intraspecific aggression, territoriality and high brood density (Williams 1974, Patterson et al. 1982, Warhurst et al. 1983, Savard 1987, Savard et al. 1998).

The accidental brood mixing hypothesis makes no specific predictions and, as such, represents a null hypothesis (Eadie & Lyon 1998). Non-random patterns of desertion and adoption therefore refute the hypothesis. Such non-random patterns of desertion and adoption have indeed been found among goldeneyes (*Bucephala* spp.) (e.g., Pöysä et al. 1997, Eadie & Lyon 1998), as well as eiders (V, Bustnes & Erikstad 1991a). Another critical feature of the hypothesis is the timing of brood mixing; mixing should only occur

before parent-offspring recognition is fully developed. However, in many geese, adoptions of unrelated goslings are common long after the development of parent-offspring recognition (reviewed in Choudhury et al. 1993, Williams 1994). In eiders, parental bonds are assumed to form between 3 and 7 days after hatching (Fabricius 1951, Munro & Bédard 1977a). Although most crèches in my study area form during the first week after hatching, observations of broods with individually marked females indicate that the system may not be as fixed as previously believed (Ahlén & Andersson 1970, Munro & Bédard 1977a, Bustnes & Erikstad 1991a, 1995), and transfer of young may also occur later in the season (unpubl. data). Furthermore, I have observed that the original broods usually reform after a temporary amalgamation episode among broods with newly hatched young (unpubl. data), which suggests that parent-offspring recognition problems are probably the exception rather than the rule.

Related to this hypothesis, is the question of proximate mechanisms of brood abandonment. Savard et al. (1998) have questioned the existence of voluntary brood abandonment in any waterfowl species (V). According to their view, some mothers may be forced to abandon their young to a more aggressive female – because they may, for some reason, be unable to strengthen their mother-duckling bonds – and that this was not their initial intent. Voluntary brood abandonment seems highly likely among goldeneyes (cf. Pöysä et al. 1997, Eadie & Lyon 1998), and has also occasionally been observed in eiders (Bustnes & Erikstad 1995, J. O. Bustnes, pers. comm.). Nevertheless, this phenomenon is extremely difficult to document in the field, at least in eiders (pers. obs.), and therefore more observational data on brood abandonment would be urgently needed (V).

Competition for brood-rearing sites hypothesis

This hypothesis assumes that post-hatch brood amalgamation occurs as an inadvertent

consequence of competition among females for brood-rearing areas. Competition results in the eviction of one female, after which the young of the defeated female mix with the winner's brood. Such a scenario has been proposed for Barrow's goldeneye (*Bucephala islandica*) and bufflehead (*B. albeola*), two highly territorial species that defend mobile brood territories for feeding (Savard 1987). This hypothesis has, however, been considered of little relevance to eiders (Bustnes & Erikstad 1991a), because they are gregarious during brood-rearing, and probably do not monopolise feeding and loafing areas (Gorman & Milne 1972, Minot 1980, Bustnes & Erikstad 1991a). Although aggression towards other females and young is common during the brood-rearing season in eiders (II), there are two arguments that can be brought up against this hypothesis. First, although brood-rearing habitats for small ducklings are restricted to the shorelines of islands (III, Hario et al. 1992), suitable patches surround most of the islands in my study area. Second, even though agonistic conflicts among broods are common during feeding, aggression is mainly directed towards the brood as a whole, i.e. tending females as well as ducklings are chased away (pers. obs.). This was also realised by Savard (1987), who found that victorious females did not attempt to steal other females' young but rather tried to chase them away or even kill them.

Alternative reproductive strategy hypothesis

Post-hatch brood amalgamation could be maintained in a population as a mixed evolutionary stable strategy (ESS) (Maynard Smith 1982). This would be the case if the two tactics, abandonment and care for young, have equal fitness payoffs and are maintained by negative frequency-dependent selection, i.e. donors of young would be most successful when the availability of brooding females was high, and least successful when there are few brooding females (Eadie et al. 1988, Bustnes & Erikstad 1991a). A mixed ESS can

be achieved in two ways: (i) individuals exhibit genetically fixed strategies (polymorphism), or (ii) individuals use strategies randomly within ESS probabilities (Parker 1984). There are two basic requirements for the hypothesis to be valid (Bustnes & Erikstad 1991a). First, a female should show consistent behaviour throughout her lifetime, e.g., either be an abandoner or a tender, otherwise there is no genetic polymorphism. Second, changes in individual behaviour should not be related to any environmental or phenotypic cue. Available data on waterfowl seriously violate these requirements. In eiders, the tending strategy of individual females is not fixed between years (V, Bustnes & Erikstad 1991a, Hario & Kekkinen in prep.). Moreover, brood abandoning and tending have been linked to phenotypic variables, such as female body weight in eiders (V, Bustnes & Erikstad 1991a, Hario & Kekkinen in prep.), and the reproductive value of the brood in goldeneye species (Pöysä et al. 1997, Eadie & Lyon 1998).

Salvage strategy hypothesis

The salvage strategy hypothesis is a composite of several subhypotheses. These subhypotheses propose different proximate explanations as the cue for brood abandonment, but they all share the same ultimate mechanism: females attempt to salvage some reproductive success when they are unable to provide parental care, or if the relative benefits of continued care are low (e.g., Lack 1968, Eadie et al. 1988).

The current breeding success of donors might be lower than would have been realised had they undertaken all aspects of the breeding effort on their own, but at least some reproductive success might be achieved. Young of abandoners have indeed been found to suffer from lower survival than young of tenders (e.g., Bustnes & Erikstad 1991a, Eadie & Lyon 1998). Five proximate factors have been proposed to influence the decision to be a donor of young: (1) limited brood habitat, (2) age and experience, (3) brood size, (4)

brood success, and (5) female energetics.

The *limited brood habitat hypothesis* states that females unable to gain access to the best brood-rearing habitats, may leave their young to the care of females with access to the best areas. Such situations could arise if high-quality brood-rearing habitat is limited. However, this seems unlikely in eiders for reasons discussed earlier (see competition for brood-rearing sites hypothesis), and it is also extremely difficult to distinguish between the competition and availability of brood-rearing sites hypotheses (Eadie et al. 1988).

The *age and experience hypothesis* predicts that young and/or inexperienced females will abandon their young to older and/or more experienced females. Another prediction is that female behaviour should change from abandoning to tending with increasing age. Age and experience play an important role in determining breeding success (reviewed in, e.g., Sæther 1990, Forslund & Pärt 1995, Martin 1995), so young and inexperienced birds may potentially be more constrained in their ability to raise a brood without risking their own chances of survival. For example, lack of breeding experience may negatively influence the amount of body reserves during nesting (Baillie & Milne 1982, Aldrich & Raveling 1983, Laurila & Hario 1988), and this in turn might affect a female's chances to rear a brood successfully. Alternatively, age and experience might be related to the dominance or broodiness of females – young birds may be more likely to lose their young to older, more aggressive females.

Existing evidence do not support the age and experience hypothesis. Brood abandonment in eiders seems unrelated to age; eider females that changed their parental care mode from one year to the next did not show any consistent trend of changing from abandonment to tending (V, Bustnes & Erikstad 1991a). Moreover, the age of eider females adopting different parental care modes has been found to be similar (Hario & Kekkinen in prep.). Correspondingly, brood desertion was not age-dependent in white-winged scoters (*Melanitta fusca*) (Kehoe 1989) or Barrow's goldeneyes (Eadie & Lyon 1998),

and in barnacle geese (*Branta leucopsis*) the tendency to adopt was not associated with age (Larsson et al. 1995).

The *brood size and brood success hypotheses* both spring from parental investment theory, which predicts that parental effort should be related to the reproductive value of the brood (Trivers 1972). The current fitness value of the brood can be split into the number of young and the survival prospects of each of them. Parents may provide more care to larger broods either because (i) the effect of brood size *per se* on reproductive value (brood size hypothesis; e.g., Nur 1984, Lazarus & Inglis 1986, Winkler 1987, Eadie & Lyon 1998), or because (ii) past mortality, reflected in current brood size, predicts future mortality of the brood and hence its reproductive value (brood success hypothesis; e.g., Carlisle 1982, 1985, Armstrong & Robertson 1988, Hakkarainen & Korpimäki 1994a, 1994b, Pöysä et al. 1997). Eadie & Lyon (1998) found support for the brood size hypothesis by showing that there is a threshold brood size below which female Barrow's goldeneyes should abandon their current brood to enhance future reproductive opportunities, although Pöysä & Milonoff (1999) call their results in question due to potential flaws in the experimental design. By contrast, Pöysä et al. (1997) found that common goldeneye (*Bucephala clangula*) females modify the duration of parental care according to the mortality already experienced by the brood, supporting the brood success hypothesis. Armstrong & Robertson (1988) found that dabbling ducks used clutch size after partial clutch removal as the cue to nest desertion, rather than initial clutch size *per se*. Pöysä (1995) further suggested that the brood success hypothesis could be applicable to a wide array of waterfowl species exhibiting brood amalgamation, including eiders.

Clutch size variation in eiders is small (I, Kilpi & Lindström 1997), and thus the value of the brood at hatching will not vary much, considering the long lifetime (Coulson 1999) and number of breeding opportunities (Coulson 1984) in the species (V). Therefore, the brood size hypothesis probably does not

apply to eiders. Circumstantial evidence also suggest that brood success may not be the key factor responsible for brood abandonment decisions. First, brood abandonment is usually a rapid process, so the time frame for assessing brood survival rates may be too short to be operative in eiders (V, Bustnes & Erikstad 1995). Second, marked females often care for broods subjected to heavy and rapid initial mortality throughout the breeding season (V). However, I do not rule out the possibility that brood success might be a factor contributing to the departure of transient crèchers from broods (II, V). Temporary brood attendance might be a reproductive tactic of the female. She may attempt to join another brood after her own brood has suffered high initial brood loss, making continued care unprofitable. By attending a crèche, her young may receive continued care, while she will soon be freed from parental duties (II). Alternatively, she may assess the survival prospects of her young after attending the crèche (V). In either case, transient crèchers should, at least in a strict sense, be classified as abandoners (Fig. 1). However, the departure of transient crèchers may also be an unintentional result of agonistic interactions within the crèche (II). Female aggression showed a peak in the early breeding season, coinciding with the decline of broods with more than two females (II). My observations indicate that it is possible that transient crèchers leave the crèche for different reasons, some females departing after being subjected to marked aggression, whereas others leave without any discernible aggression preceding the departure (unpubl. data).

According to the *energetic salvage strategy hypothesis*, females in poor body condition abandon their brood, thereby increasing their lifetime fitness at the expense of a single season's breeding effort. Brood abandonment entails definitive advantages to female eiders in poor condition in the northern Baltic (III). While females tending small young are forced to feed primarily on gammarids, brood abandoners feed on the preferred prey, blue mussels (III). This preference for mussels is highlighted by the observation that individu-

ally known females switched to a mussel diet immediately after losing their brood (III). Gammarids are non-preferred food either because they (i) offer a lower energy intake rate, or because they (ii) function as an intermediate host for the acanthocephalan intestinal parasite *Polymorphus minutus*, thereby predisposing eider females to infection that can be potentially dangerous if the host's resistance is low (III). Blue mussels may offer eiders an even energy return (see Guillemette et al. 1992, Guillemette & Himmelman 1996) because they occur in high biomass in the Baltic (I), but unfortunately no data exist on the energy intake rate of birds feeding on mussels and gammarids, respectively. Though the importance of *Polymorphus* infection is controversial (Hario et al. 1995), infections can be destructive for eiders in poor condition (Hollmén et al. 1996, 1999), such as females suffering from breeding anorexia. Furthermore, it has recently become clear that the prevalence and intensity of parasite infection often increases in animals that are reproducing, and that this may be an important pathway for the cost of reproduction (e.g., Sheldon & Verhulst 1996, Deerenberg et al. 1997, Wiehn & Korpimäki 1998). Reproductive effort in eider females may increase susceptibility to parasite infection and, in addition, immunocompetence may be reduced due to adaptive reallocation of resources in times of increased energetic demand (Deerenberg et al. 1997), such as the post-hatching period in female eiders. Thus, animals may engage in behaviours that reduce the likelihood of becoming exposed to parasites (Christe et al. 1994, Sheldon & Verhulst 1996).

My results clearly upheld the prediction of the energetic salvage strategy hypothesis (V). First, females generally tended to abandon more often in years when average female body condition was low (Table 2 in V, Bustnes & Erikstad 1991a, Hario & Kekkinen in prep.). Second, abandoners had the lowest condition index of all female categories (Fig. 1 in V). Bustnes & Erikstad (1991a) also found a significant body weight difference between abandoners and tenders, albeit this

difference was only significant in one (poor) year out of three, when years were analysed separately. Nevertheless, tenders were consistently heavier than abandoners in all three years of the study by Bustnes & Erikstad (1991a). Moreover, as Bustnes & Erikstad (1991a) used a two-week timeframe for assessing brood abandonment instead of using only 7 days as I did (V), they were probably unable to distinguish transient crèchers from “true” abandoners. Third, mean body weight at hatching among females that changed behaviour from one year to another, was higher with marginal significance in the year when they cared for young than when they abandoned their young (V). Bustnes & Erikstad (1991a) obtained similar results, though they did not statistically test this difference due to small samples. Furthermore, the body weight of females that did not change behaviour was similar between years (V). In an experimental study, body condition of arctic puffin (*Fratercula arctica*) parents was found to be an important factor in the decision to desert the chick (Johnsen et al. 1994). In contrast, Kehoe (1989) found no evidence that female white-winged scoters in poor condition abandoned their young more often than females in good condition.

Why be a recipient of young?

Constraint hypothesis

Providing care to unrelated offspring could entail fitness costs to the recipient, in terms of reduced post-hatch survival of own young, or reduced survival of the alloparent itself (Eadie et al. 1988). A female may be unable to avoid these costs due to behavioural or genetic constraints. Three main categories of constraints have been proposed: (1) learning constraints, (2) repulsion constraints, and (3) hormonal constraints.

Caring for unrelated young may be the inadvertent consequence of poor parent-offspring recognition (e.g., Riedman 1982, Tella et al. 1997, Brown 1998). The *learning con-*

straint hypothesis is therefore related to the accidental brood mixing hypothesis for brood abandonment. However, an alloparent may occasionally accept strange offspring though it is capable of discriminating between own and alien young – such a situation could arise if the costs of rejection become too high relative to the costs of accepting additional young (e.g., Saino et al. 1994, Redondo et al. 1995). For example, the only other option for a parent may be to abandon the whole brood (Eadie et al. 1988), or engage in activities such as parental infanticide, which by mistake may hit its own offspring if offspring recognition is poorly developed (Brown 1998). This is the rationale of the *repulsion constraint hypothesis*.

Accepting unrelated young might also be a consequence of misdirected parental care. Cases of interspecific adoption clearly demonstrate that such behaviour does exist (e.g., Riedman 1982). Helping behaviour is mediated by prolactin (e.g., Schoech et al. 1996, Brown & Vleck 1998), and alloparenting might be explained by endocrinological mechanisms allowing the birds to be exploited by young soliciting food or brooding (Jouventin et al. 1995). However, Schmutz et al. (1982) found that the levels of circulating prolactin in non-breeding eider females attending crèches were low and similar to the basal level of males. These results did therefore not support the *hormonal constraint hypothesis*.

Is adoption of extra young really costly to parents? While there is convincing evidence in altricial birds that young in larger families suffer from increased mortality (reviewed in Lindén & Møller 1989, Dijkstra et al. 1990), the evidence in semiprecocial and precocial species is equivocal. However, females often show marked aggression towards unrelated young (e.g., II, Redondo et al. 1995, Eadie & Lyon 1998, Savard et al. 1998), indicating some potential cost of adoption. A few studies have indeed reported a decreased survival of own offspring (e.g., Williams 1974, Safriel 1975, Saino et al. 1994, Dzus & Clark 1997, Brown 1998), or lowered female body condition (Lessells 1986) as a consequence of

adoption and/or augmented brood size. Dzus & Clark (1997) suggest that brooding efficiency in mallards (*Anas platyrhynchos*) may constrain duckling survival in large broods. However, inadequacy of the brooding system is probably a minor cause of mortality in eiders, because only c. 5% of newly hatched young were potentially exposed to chilling due to unfavourable high ratios of ducklings to brooding females (II, see also Mendenhall 1979).

Neutral effect hypothesis

Pierotti (1988) suggested that adoption should be less costly to parents in precocial species, where parental care mainly consist of guarding and brooding the young, and the young feed themselves. A number of studies have reported a neutral effect of accepting additional young on parental fitness. Thus, brood size has been found to be unrelated to duckling survival (e.g., Mendenhall & Milne 1985, Rohwer 1985, Lessells 1986, Bustnes & Erikstad 1991a, Afton 1993, Larsson et al. 1995, Eadie & Lyon 1998, Milonoff et al. 1998), or female survival (e.g., Afton 1993, Williams et al. 1994, Larsson et al. 1995).

Benefit hypothesis

The costs of accepting additional young may be so negligible in precocial species, that adoption may enhance, rather than reduce, the fitness of the recipient (Riedman 1982, Eadie et al. 1988). Increased duckling survival with increasing brood size has been reported in several precocial species (e.g., Cooper & Miller 1992, Williams 1994, Lanctot et al. 1995, Lepage et al. 1998, Loonen et al. 1999), including the eider (Munro & Bédard 1977b), while some studies have also reported an increase in adult condition or survival with increasing brood size (Williams 1994, Loonen et al. 1999). Benefits could accrue to the alloparent due to (1) exploitation of fostered young, (2) parenting experience, (3) reciprocal altruism or kin selection, (4) enhanced

dominance, or (5) selfish interests.

Exploitation of fostered young could be the outcome of the dilution effect, or safety in numbers – the probability of a certain individual being captured by the predator decreases with increasing group size (Bertram 1978). Second, additional females and young may facilitate rapid detection of a predator, and large numbers of prey may also confuse and disrupt predator attacks through the confusion effect (Bertram 1978). Third, parents might actively exploit adopted young by means of the selfish herd effect, i.e. the survival of own young is disproportionately high in comparison to unrelated young (Hamilton 1971). Nastase & Sherry (1997) found that adopted Canada goose (*Branta canadensis*) goslings were located further away from female adults, and showed decreased survival compared to natural goslings, which is consistent with the selfish herd effect. However, in my view, nothing in the behaviour of eider females points in the direction that they would treat ducklings differently within a brood (pers. obs., see also Bustnes & Erikstad 1991a). Finally, larger broods might aid in predator defence, e.g., by shared predator mobbing (Lanctot et al. 1995). Although eider ducklings themselves do not participate in predator defence, the multi-female tending strategy of eiders may enable more efficient predator deterrence (V, Munro & Bédard 1977b, Minot 1980). The efficiency of predator defence is, however, related to the ratio of ducklings to tending females in the eider crèche, and not to the number of ducklings *per se* in larger broods containing adopted young.

Parenting experience has been proposed as one explanation of alloparenting, especially in mammals (Riedman 1982, Emlen & Wrege 1989, Emlen et al. 1991). Some females in eider crèches demonstrably belong to the non-breeding cohort (Schmutz et al. 1982, Bustnes & Erikstad 1991b). It intuitively seems difficult to imagine that the benefits of enhanced parenting experience would outweigh the costs of skipping one breeding season altogether in non-breeders, with the possible exception of immature females with

no prior breeding experience.

Reciprocal altruism and *kin selection* have been invoked to explain cooperative breeding in many altricial birds and mammals (e.g., Eadie et al. 1988, Emlen & Wrege 1989, Emlen et al. 1991). Female waterfowl possess many of the prerequisites for kin selection or reciprocity to evolve (see Habitat use). Furthermore, the dispersion pattern of post-nesting eider females was such that females forming crèches probably originate from the same colony (IV, see also Habitat use).

One possible advantage of adoption is *enhanced dominance* owing to group size effects (Emlen & Wrege 1989, Emlen et al. 1991). Larger families may dominate over smaller ones, because brood size *per se* affects the motivation of parents during agonistic interactions, making larger family units stronger competitors for food. Such brood-size dependent dominance is particularly well-developed among geese (reviewed in Loonen et al. 1999, see also Habitat use). The fitness gains of enhanced dominance in geese may be so pronounced that survival, size and mass of ducklings, as well as adult body mass, may be enhanced (e.g., Lepage et al. 1998, Loonen et al. 1999). Equally strong effects of group size on fitness are hardly to be expected among eiders, which are less territorial, and where intraspecific competition for food is less strong. Nevertheless, to explore the relationship between social dominance and the number of ducklings and tending females in eider broods would certainly be of high priority (IV).

Selfish interests include advantages accruing only to the female participating in post-hatch brood amalgamation. Such benefits could entail, e.g., avoidance of predation or kleptoparasitism (Bustnes & Erikstad 1991b, Bustnes 1993), or improved feeding success. I set out to test a hypothesis whether joint care in female eiders may allow females flexibility as to feeding method and site, while still participating in brood care (III). More specifically, I explored whether the feeding behaviour of multi-female tenders might reveal that these females could avoid unprofitable prey, gammarids, to a larger extent than lone ten-

ders (see Salvage strategy hypothesis). I did not find any significant differences in the feeding habitat, feeding mode, or dive duration of lone tenders and multi-female tenders (III). However, multi-female tenders took an intermediate position between lone tenders and females without young regarding all measured feeding behaviour variables (III), so larger sample sizes might potentially have revealed some differences. It is also possible that the total activity budgets of lone tenders and multi-female tenders differ (III). For example, a female could be able to allocate more time to feeding, and decrease the level of personal vigilance, when there are more tending females in the crèche (see Bertram 1980). A larger allocation of time to feeding, in combination with an increased rate at which food patches are located, usually leads to a positive relationship between group size and mean food intake rate in birds (reviewed in Beauchamp 1998a).

Evolution of amalgamation behaviour: synopsis of plausible explanations

Summing up the pros and cons of the proposed hypotheses for post-hatch brood amalgamation, it seems that the salvage strategy hypothesis *sensu lato* is the most plausible explanation of brood abandonment in waterfowl. Why should this be so? One general explanation is that adults of long-lived species, such as seabirds and waterfowl, may be less prone to trade their own survival for that of their offspring (Lindén & Møller 1989, Clark & Ydenberg 1990, Erikstad et al. 1998). Even a small reduction in adult survival would reduce the number of subsequent breeding attempts, thereby greatly lowering lifetime reproductive success. By contrast, it is far less clear whether acceptance of unrelated offspring is costly, of neutral adaptive value, or beneficial to waterfowl. Most evidence indicate that adoption in precocial species seems to entail only minor costs to recipients. The

actual balance between costs and benefits of adoption is closely interrelated to the behaviour of the particular species under study, as exemplified by the brood-size dependent dominance hierarchy in geese, which translates into a clear-cut benefit of adoption.

If we scrutinise the proximate factors influencing parental care decisions on a species level, a clear picture emerges: different proximate mechanisms apply to different species. For example, the energetic salvage strategy hypothesis for brood abandonment is valid for eiders (e.g., V), whereas the brood success (Pöysä et al. 1997) or brood size (Eadie & Lyon 1998) hypothesis may be applicable to goldeneye species. Why do we find such species-specific differences? The reason is probably related to the different life history strategies of the species. Explanations based on energetic considerations may apply to eiders, with a high degree of reliance on nutrient and energy reserves for breeding. By contrast, explanations based on brood value may be suited for species with a comparatively large variation in clutch and brood size (see Pöysä et al. 1997), but with only a minor degree of reliance on reserves for breeding, such as goldeneyes. The conclusion is that the relative importance of different proximate mechanisms underlying parental care decisions varies greatly between species.

It is probably unrealistic to assume that only one factor determines parental care decisions; several factors may act in combination. For example, Erikstad et al. (1993) showed that brood abandonment in eiders was related not only to female body condition (energetic salvage strategy hypothesis), but also to clutch size (brood size hypothesis) – females hatching large clutches tended their brood at a lower body mass than females hatching small clutches. However, I did not find any difference in clutch size between abandoners and tenders (V). Another example comes from clutch abandonment in king penguins (*Aptenodytes patagonicus*) (Olsson 1997): abandonment depended on body condition, but it was also state-dependent, so that experienced birds abandoned their clutch at a nearly significantly lower body mass than inexperi-

enced birds (age and experience hypothesis). Olsson (1997) concluded that experienced birds are more proficient foragers and therefore able to better compensate for low body reserves. In this respect, it is unfortunate that neither Pöysä et al. (1997) nor Eadie & Lyon (1998) did consider female body weight as a factor that might potentially influence brood abandonment in goldeneyes, in addition to the reproductive value of the brood.

The debate on proximate and ultimate mechanisms of post-hatch brood amalgamation has conventionally been polarised into two extremes; one approach centred on benefits to donors, recipients or for the young themselves, the other approach regarding crèching as a nonadaptive epiphenomenon (see Eadie & Lyon 1998). Eadie & Lyon (1998) recently tried to uncouple the processes of brood abandonment and adoption. They argued that crèching was primarily driven by the parental investment decisions of the donor parent, and that adoption of young was the secondary outcome of selection acting on deserted offspring to find another brood to join. As such, brood amalgamation behaviour would entail parent-offspring conflict over brood abandonment and an intergenerational conflict (*sensu* Pierotti & Murphy 1987) over adoption of abandoned young. Brood abandonment in waterfowl seems to involve an element of parent-offspring conflict – the abandoning parent uses a proximate factor such as body condition or brood success as the cue for brood abandonment, so as to increase its lifetime reproductive success. From the ducklings' point of view abandonment is almost always detrimental, because their survival would probably have been better had the female continued to care for them (e.g., Bustnes & Erikstad 1991a, Eadie & Lyon 1998). However, adoption seems to entail only slight, if any, costs to the recipient in many waterfowl. At least in geese it is probably inappropriate to talk about adoption in terms of an intergenerational conflict, because both adopted ducklings *and* adopting parents may benefit (Williams 1994). Waterfowl fit the prediction of Pierotti (1991), who suggested that adop-

tion should be common and infanticide non-existent in species with little or no cost to adoption.

Finally, it is interesting to speculate about the special features of post-hatch brood amalgamation in eiders. Why are eiders unique among waterfowl by exhibiting joint care by several females, and how has this trait evolved (V)? It seems plausible to assume that the original care mode in eiders was lone tending, and that lone tenders occasionally accepted extra young, which is a common feature among many waterfowl. Characteristics of eiders such as coloniality, longevity, and philopatry may have constituted pre-adaptations necessary for joint female care to evolve. The benefit of joint brood care could be further enhanced if reciprocity or kin selection would play a role in brood amalgamation (V).

Open questions and challenges for the future

As is typical of science, my work has brought to light far more open questions than it was able to answer. In this section I will briefly identify and discuss some of them. I will also try to foreshadow some fruitful ways of approaching these questions.

One apparent shortcoming in paper I was the lack of female pre-laying body weights. Therefore I was unable to rigorously test the association between clutch size and reserve size. This relationship is expected to be positive in capital breeders (Ankney & MacInnes 1978, Thomas 1988). This problem is, however, difficult to overcome until more efficient live-trapping methods are developed; large-scale collecting of pre-laying females (e.g., Ankney & MacInnes 1978) is a thing of the past in my opinion. Another important issue would be to explore the energy- and nutrient-reserve dynamics of breeding male waterfowl. Male reproductive bioenergetics have so far been neglected, although males may pay energetic costs equalling those of females during breeding (reviewed in Hipes &

Hepp 1995).

Another question of fundamental importance is the distinction between lone tenders and multi-female tenders. Do lone tenders and multi-female tenders differ with respect to, e.g., social dominance or body condition (II, III, IV, V)? Regarding dominance relationships, detailed field observations of clashes between broods and crèches would certainly be useful. It would be especially rewarding to distinguish between the effect of brood size *per se* (i.e. number of ducklings), and the effect of female number, on inter-brood dominance relationships. It should also be possible to experimentally examine the relationship between brood size and dominance, by exchanging eggs (cf. Lepage et al. 1998) or newly hatched ducklings (cf. Loonen et al. 1999) between nests, thereby creating enlarged and reduced broods. Such an experiment would also provide us with useful information about the influence, if any, of brood size on abandonment decisions in eiders.

The question whether lone tending and multi-female tending are related to female body condition was left essentially unanswered (II, V). The largest data set revealed no significant differences in condition between these two categories of females, although lone tenders tended to have the highest mean condition index (V). Thus, the observation that multi-female tending was proportionally more common two weeks after peak hatching in years when average female body condition was low (Fig. 4, II), could possibly be explained by the slight but statistically insignificant difference in body weight between lone tenders and multi-female tenders. But why then should lone tenders initially be less common in years when average female body condition is high (Fig. 4, II)? The first brood census may be particularly sensitive to minute deviations in the timing of censusing in comparison to the median hatching date in the population, because brood structure is most variable at that time (II). Therefore the relatively high proportion of lone tenders in the first census in poor years might merely be an artefact. Alternatively, the

incidence of lone tending and multi-female tending may vary as a function of some unknown extrinsic factor, which in turn might be related to female body condition at hatching. Nest density is a key determinant of pre-hatch brood amalgamation (Robertson 1998), and it may also influence the opportunities for post-hatch brood amalgamation, given that high nest density enhances the likelihood of brood encounters after hatching (II). The breeding population at Tvärminne has remained fairly stable, so nest density *per se* probably does not contribute much to the between-year variation in tending strategies (II). However, incorporation of nesting synchrony in the analysis of annual tending strategy patterns might prove to be rewarding.

It may seem a mystery why many brood abandoners and failed nesters stayed close to their nesting island throughout the breeding season, considering that they feed on blue mussels, and these were far more abundant further out at sea (IV). What benefits could these females possibly gain by staying sedentary rather than moving to better feeding grounds? The simplest reason would be conspecific attraction (e.g., Pöysä 1992, Beauchamp et al. 1997) towards other feeding conspecifics close to the colony, but this explanation certainly seems insufficient in this case. An alternative explanation is that these females could be monitoring the current reproductive success of other females from the same colony, and use this information as a cue to select their nest site during subsequent breeding attempts (e.g., Schmutz et al. 1982, Cadiou et al. 1994, Boulinier et al. 1996, Danchin and Wagner 1997). Eider females that nest unsuccessfully tend to change nest site (Milne 1974, Bustnes & Erikstad 1993), and the rate of partial and total nest predation is c. 20% in my study area (pers. obs.). We may speculate that access to a specific nest site the next season would require that the prospecting female is present at the colony for most of the breeding season.

As suggested several times in my thesis work (IV, V), the pursuit of clarity regarding the role of kin selection and reciprocity would

be a necessary and logical next step in the study of brood amalgamation behaviour in waterfowl. The technical tools to assess kinship in eiders are already there – microsatellites are probably the best available method at the moment (C. R. Primmer, pers. comm.), and at least seven PCR primers functional for eiders are published (Fields & Scribner 1997). If kin selection plays a part in crèching behaviour, we can make the following predictions of average relatedness among eider females:

$$\text{relatedness}_{\text{within crèche}} > \text{relatedness}_{\text{within-colony}} > \text{relatedness}_{\text{between-colonies}}$$

Even though these predictions would not be met, reciprocity may still operate in brood amalgamation behaviour. As shown by Ekvall (1999), it is also possible for both kin selected and reciprocal parental care behaviours to operate simultaneously within the same population.

While collecting data in the field, I have observed phenomena that I have barely touched upon in my thesis work. One of the most puzzling questions from an evolutionary point of view is, why usually two broody females join together, whereas stable coalitions with three or more females are more seldom observed (II, Bustnes & Erikstad 1991a). Elucidation of the costs and benefits of brood amalgamations involving different numbers of participating females would definitely be an important goal of future research.

Circumstantial evidence, though so far based on scanty data, also indicates that it is possible for some broody females to practice role partitioning within the brood. One female might, e.g., be responsible for aggression and brood defence, whereas the other female may take on most of the responsibility for brooding and leading the young (pers. obs., J. O. Bustnes, pers. comm.). If role partitioning of females within a crèche does occur, it would mean the death-blow for non-adaptive explanations of crèching behaviour involving stable multi-female care (cf. Emlen et al. 1991).

Conclusions

I have shown that local food resources had a large effect on the pre-laying foraging behaviour of eider females breeding in the northern Baltic, yet local food resources seem to play a minor role in determining clutch size (I). This apparent paradox may be explained by the high degree of reliance on energy reserves exported from the wintering quarters. Capital breeding also seems to buffer nesting females against deteriorating food conditions in the Gulf of Finland, but the high degree of philopatry of females currently appears maladaptive in the population, because recruitment is low and the population is declining in the central and eastern parts of the Gulf of Finland (I).

The structure of eider broods showed a regular pattern of within-season change, and a distinct pattern of between-year variation (II, V). Brood structure was most variable initially (II), with multi-female tending invariably being the most common mode of care (II, V). Broods with more than two tending females rapidly decreased in frequency (II), coinciding with the departure of transient crèchers from broods (V). Transient crèchers may leave the broods due to aggression within the brood (II), or this behaviour may represent a reproductive tactic of the female, involving assessment of the reproductive value of her brood (II, V, see also Pöysä et al. 1997). The proportion of lone tenders increased, and the proportion of two-female broods was stable, throughout the rearing season (II). The number of females in broods remained roughly stable apart from the variable phase following hatch, indirectly indicating stability (II). The between-year variation in tending strategies was related to average female body condition in a predictable manner (II). However, the interplay of tending strategies and body condition is far from being resolved, as a later analysis revealed no significant differences in body condition between lone tenders and multi-female tenders (V). Lone tenders appeared to be in slightly better condition, which might explain why multi-female tending was relatively more common in

years when average female condition was low, two weeks after hatch (II). I also found the seemingly contradictory result that lone tending was less common initially in years when average condition was high (II). Besides being an artefact, this finding may also denote that some other extrinsic factor, possibly related to female body condition, may be important.

Female breeding status appeared to have only a minor impact on the post-nesting site use and movements at large (IV). However, if we consider female habitat use, feeding technique, and diet on a finer spatial scale, females caring for small young are clearly constrained compared to females without young (III). Post-nesting eider females aggregated close to their breeding colony, and females from different colonies were essentially spatially separated (IV). This dispersion pattern may imply a benefit of familiarity with brood-rearing areas, but the apparently strict separation of females from different colonies is more difficult to explain – it may result from females solely moving to the nearest available feeding site, but as all females obviously do not do this, mutual avoidance or aggression of females might also play a role. One consequence of this dispersion pattern is that females participating in brood amalgamations may originate from the same colony, which may have important implications considering the high degree of female philopatry.

I found that the predictions of the energetic salvage strategy hypothesis for brood abandonment were upheld with respect to eider females. Thus, abandonment was more common in years when average female body condition was low, brood abandoners had the lowest condition index, and body weight at hatching among females that changed parental care behaviour from one year to another, was higher when caring for young than when abandoning (V). Brood abandonment involves advantages to eider females in poor condition, because these females may avoid unprofitable prey used by small ducklings and brood-caring females (III).

Whether adopting extra young is costly or beneficial in eiders remained an unresolved

issue. The frequent aggression of females towards unrelated young indicates some potential cost of adoption (II). However, several tending females should offer better protection against predation (V, Munro & Bédard 1977b, Minot 1980), given that the ratio of ducklings to tending females is sufficiently low. Crèching behaviour might also offer benefits to the females themselves. I tested whether females might achieve some foraging benefits by tending together, while still participating in brood care (III). The results were equivocal: there were no significant differences between lone tenders and multi-female tenders regarding feeding method and habitat (III). However, the potential benefit accruing to multi-female tenders may also manifest itself as a difference in total activity budgets, with differing allocations of time to different activities.

How general are my results, and to what extent can they be generalised to other species? Perhaps my most fundamental finding was the variety of explanations pertinent to different species regarding, e.g., post-hatch brood amalgamation. The eider is undoubtedly exceptional in many respects, even among waterfowl, so the generality of my results appears rather limited at first sight (cf. Eadie & Lyon 1998). However, only by comparing species differing greatly regarding, e.g., post-hatch brood amalgamation behaviour, might we receive a greater understanding of the relevant life history traits responsible for variation in this behaviour. As an example, I found in my review of literature that the salvage strategy hypothesis for brood abandonment *sensu lato* appears the most widely applicable to waterfowl. This may be explained by the reluctance of long-lived adult waterfowl to trade their own survival for that of their offspring (Lindén & Møller 1989, Clark & Ydenberg 1990, Erikstad et al. 1998). However, the proximate mechanisms responsible for abandonment decisions seem to differ among waterfowl species, due to different life history strategies. Explanations based on energetics may be important for eiders, whereas species mainly relying on exogenous nutrients, with a large variation in clutch and

brood size, may base abandonment decisions primarily on brood value.

I have pin-pointed several important areas of future research. To mention but a few, I would like to emphasise the determination of the role of kinship and reciprocity in brood amalgamation, the possibility of role partitioning among females within a brood, inter-brood dominance relationships as a function of the number of females and ducklings, and the value of staying sedentary at the colony for failed nesters and brood abandoners. Last but not least, we should not forget the reproductive bioenergetics of males, the neglected sex in my thesis work.

Above all, this thesis work has demonstrated the dangers of being obstinate in defending only one particular hypothesis or explanation. When evaluating the general applicability of our results, we should pay careful attention to the immense variation in life history strategies exhibited by individual species. Ideally, we should also endeavour to test among several competing hypotheses, because more than one factor may co-operate even within the same species. Keeping these facts in mind, much of the unnecessary controversy that has characterised the ongoing debate, could be avoided in future.

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