Why should Greylag Goose *Anser anser* parents rear offspring of others?

L. Nilsson & H. Kampe-Persson

Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden.
leif.nilsson@zooekol.lu.se, hakonpersson@hotmail.com

The benefits and costs of rearing large broods were studied in a population of neck collared Greylag Geese in Scania, southernmost Sweden. Families were divided into four groups according to brood size: 1-4, 5-8, 9-12 and >12 young. Gosling survival showed a significant positive relationship with brood size on arrival at the rearing area. First-year and third-year local survival, as well as breeding recruitment, showed a significant positive relationships with brood size at fledging. For adults rearing large broods, no costs were detected during the year following that when they fledged >8 young; both survival rate and reproductive success exceeded the long-term averages.

Key Words: neck collared population, adoption, survival, recruitment, south Sweden

Greylag Geese *Anser anser* are sometimes seen with very large broods of small young, some broods being so large (up to 55 young) that it is impossible for a single female to have incubated so many eggs (Karlsson *et al.* 1982; Jensen 2000; Persson 2002). It is well-known that Greylag Geese, like a number of other waterfowl species, sometimes lay their eggs in the nest of another female, but excessively large clutches laid by two or more females rarely hatch (Hauff 1982; Witkowski 1983). In addition to these very large broods, there are also many cases where just one or two eggs are added to a clutch, or one or a few young are adopted into a brood.

The habit of intra- and inter-specific egg parasitism and the adoption of small young is widespread among different species of waterfowl (Eadie *et al.* 1988; Lank *et al.* 1989; Weigmann & Lamprecht 1991; Williams 1994; Beauchamp 1997; Andersson & Åhlund 2001). The adoption of foreign young is a prevalent habit of the Common Eider *Somateria mollissima* and has been studied by a number of workers, who have discussed the advantages for females that leave their young in the care of others (eg Bustnes & Erikstad 1991; Pöysä 1995; Kilpi *et al.* 2001; Bustnes *et al.* 2002). Eadie & Lumsden (1985; cf. also Amat 1987) concluded that nest parasitism would sometimes not be disadvantageous for the host but might be of advantage.

Modern DNA techniques have revealed that there is a high frequency of mixed parentage due to nest parasitism and adoption of young both in ducks (Andersson & Åhlund 2001) and geese (Choudhury *et al.* 1993; Larsson *et al.* 1995). Among geese, parental care in the form of vigilance and protection can serve all members of a brood, and the acceptance of extra young would therefore have no negative effects on the host family (Lazarus & Inglis 1986). Cooch (1991) found a faster growth rate in large families and suggested that the adoption of young could lead to positive effects for the host family. Larger families have a better chance of detecting predators at an early stage, and the strategy of adopting foreign goslings may dilute the predation on their own offspring (Eadie & Lumsden 1985; Eadie *et al.* 1988). Larger families are socially dominant over smaller families (Black & Owen 1989; Boyd 1953; Hanson 1953; Raveling 1970), which was found to be of advantage in wintering Lesser Snow Geese *Anser caerulescens caerulescens* (Gregoire & Ankney 1990).

In this study, these questions are addressed for the Greylag Goose by studying pre- and post-fledging survival rates and recruitment rate in a neck collared population that had been studied intensively since 1985.

Study population

The study population has never been manipulated during nesting, because of the risk of influencing the breeding performance (cf. Witkowski 1983).

Pre-hatch brood amalgamation has not been studied in this population. For the present, there is only circumstantial evidence of pre-hatch brood amalgamation, such as the occurrence of nests containing >12 eggs and the nest of a Barnacle Goose *Branta leucopsis* which contained four of its own eggs and six Greylag Goose eggs (Nilsson & Persson 1994; Persson 1997). A clutch of 12 eggs is widely accepted as the largest a Greylag Goose could lay naturally (Kampe-Persson 2002). In a German study, 7% of 467 nests contained >12 eggs, and 18% of all eggs were found in nests containing 13-40 eggs (Hauff 1982). In a Polish study, only two clutches out of 629 contained >12 eggs; all clutches containing 1-6 eggs were laid by a single female, while more than half of those containing 9-12 eggs were laid by two females (Witkowski 1983). Overall, 4% of all nests contained eggs laid by two females; in 30% of these, two females had laid two complete clutches in a single nest, while in the remaining 70%, one female had laid a complete clutch and another female had added 1-3 eggs. The Swedish study population, established in the late 1960s, grew on average 15.3% per annum (Nilsson *et al.* 2002), and now numbers >1,000 breeding pairs. As a consequence, pairs nest close together, either in reedbeds or on small islands (Nilsson & Persson 1994), which increases opportunities to lay eggs in other females' nests (Brown 1984). Consequently, there is no reason to assume pre-hatch brood amalgamation to be less frequent in the study population than in other goose species (Lank *et al.* 1989; Weigmann & Lamprecht 1991).

Almost all families with >12 young formed before they reached the rearing area, and early-formed broods always consisted of similar-aged goslings (Persson 2002). In the rearing areas, on the other hand, permanent brood mixing was an extremely rare event, while pairs frequently lost or gained one or a few goslings. Warhurst & Bookhout (1983) suggested that post-hatch brood amalgamation in Canada Geese *Branta canadensis* occurs due to accidental brood mixing shortly after hatching in areas of high brood density. The same seems to apply to the study population.

During the study period, the most common brood size of families arriving at the rearing area was five, but four was almost as common (**Figure 1**). The commonest brood size at fledging was three, closely followed by two and four young. The largest brood seen during the study had 27 young, followed by

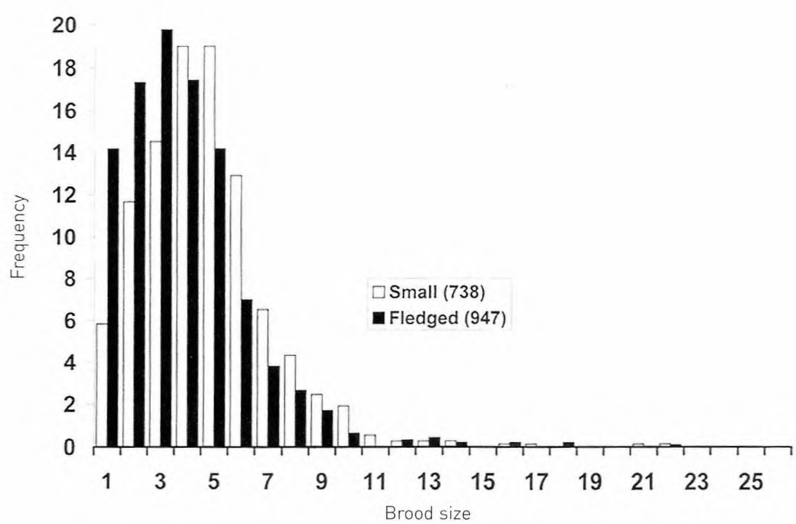

Figure 1. Distribution of brood sizes in the study area, Scania, south Sweden, on arrival to the brood-rearing area (light columns) and at fledging (dark columns), pooled over 1984-2002. All families having at least one neck collared parent were included.

families of 22, 21 and 17 young. The largest family at fledging had 22 young. A total of nine broods numbering >12 young when first seen at the rearing area was found, six at Lake Yddingen and three at Lake Börringesjön. The mean number of young in these broods decreased during brood-rearing, from 17.4±1.63 to 14.6±1.49.

Method

Greylag Goose families were captured and neck collared annually in a study area in southwestern Scania, southernmost Sweden, from 1985 onwards (Nilsson & Persson 1992; Persson 1994). A total of 575 adults and 1,700 goslings had been neck collared by 2000 (Persson 2000a). Goslings were neck collared on average 22±0 days before they fledged (Nilsson *et al.* 1997). Individuals marked with poor quality neck collars (mainly 1984-1985) were excluded from the analyses (cf. Persson 2000b).

During 1985-2002, regular searches for neck collared geese were undertaken from their arrival in spring until their autumn departure. In spring, the study area was visited several times a week in order to establish the return of marked birds and their breeding performance. From late May until the last young were fledged, the breeding area was visited almost daily to establish the number of fledglings in each family. In summer and autumn, weekly searches were extended to include neighbouring staging areas, especially the Foteviken area on the coast, where a large proportion of the Greylag Geese from the study area gather (cf. Nilsson & Persson 1992).

For analysis, families were divided into four groups according to brood size, on arrival at the rearing area and at fledging, respectively: 1-4, 5-8, 9-12 and >12 young.

Rearing survival was expressed as the number of geese that fledged as a percentage of the number that had reached the brood-rearing area. Calculations were based on the number of young in families having at least one neck collared parent. All such families recorded in a rearing area within ten days of hatching were included. Account was taken of pairs that lost all their young and left the study area to moult elsewhere, as well as of pairs that left the main rearing area before fledging. Permanent brood mixing was accounted for by assuming that gains and losses of goslings were independent of family size. In this way, survival estimates were not influenced as the individual was used as a sampling unit when following changes in brood size. During the latter half of the rearing period, goslings commonly left their parents without joining another family for shorter or longer periods (up to three weeks), but all recorded separations ended with a complete re-grouping of the family. As significantly fewer small young survived to fledging at Lake Fjöllfotasjön than at the three lakes, Klosterviken, Börringesjön and Yddingen (45% vs 68-

71%; Nilsson *et al.* 2002), only families from the latter three lakes were included in the analysis.

First-year and third-year local survival were expressed as the number of geese re-sighted after 1 July in years t+1 and t+3 respectively, as a percentage of the number that fledged in year t. Such a simple method was possible because of the extremely high re-sighting frequency of all groups of geese (Nilsson & Persson 1993), supporting the assumption that the probability of detecting a surviving neck collared individual present in southwest Scania after the cut-off date (1 July) equals one. The resulting estimates were probably slightly lower than the true survival rates as they took into account neither early natal dispersal to sites outside southwest Scania (Nilsson & Persson 2001a) nor neck collar losses (Persson 2000b). In this study, underestimates of the true survival rates were assumed to be evenly distributed over brood sizes, small and of no importance for the outcome of the analyses.

Greylag Geese were considered to be recruited to a breeding area if they were seen with a nest or unfledged young in the area (Nilsson & Persson 2001a). In addition, geese seen during the first two weeks after fledging were considered to be recruited to the same area. Most individuals had recruited to the breeding population ny the time they were five years old, but new parents were often unsuccessful. A paired bird in the fifth calendar year was counted as recruited to a site if it remained faithful to it.

Results

Rearing survival

The survival of young during brood-rearing was significantly higher with increasing family size (**Figure 2**; χ^2_3=17.94, P<0.001). Restricting the analysis to lakes and years when broods of >12 young were recorded, the outcome did not change: differences were still highly significant (χ^2_3=17.98, P<0.001).

Local survival rates

Both first-year and third-year local survival were significantly higher with increasing family size (**Figure 3**; χ^2_3=16.11, P<0.01 and χ^2_3=9.31, P<0.05, respectively).

In an earlier study, Nilsson *et al.* (1997) showed that survival rates differed among lakes. Making the analysis separately for the four main study lakes, the same general pattern was found in all lakes but differences were significant only at Lake Yddingen, for first-year as well as third-year local survival (n=461; χ^2_3=9.32, P<0.05 and χ^2_3=8.71, P<0.05, respectively).

Recruitment rate

The recruitment rate, when calculated for all fledged young, was significantly higher with increasing family size (**Figure 4**), for all (χ^2_3=13.38, P<0.01) as well as for successful (χ^2_3=13.26, P<0.01) recruits. Restricting the analysis to birds surviving at least

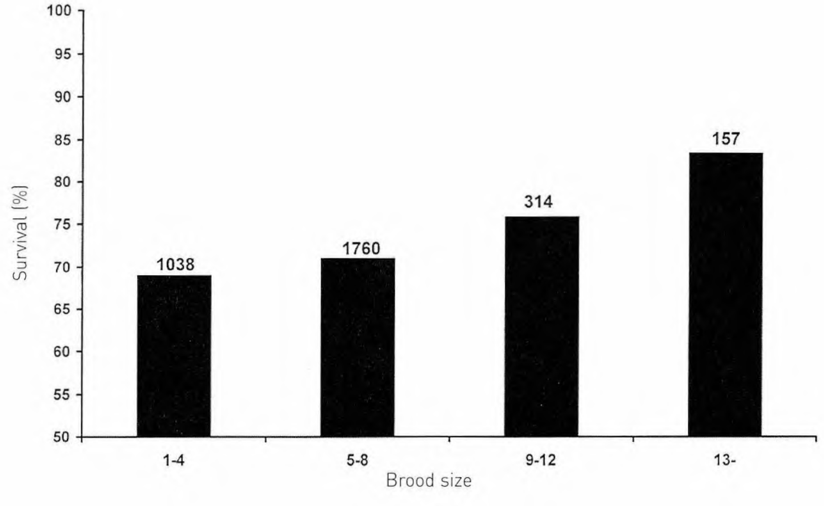

Figure 2. Survival (%) of young during brood-rearing in relation to brood size on arrival at the brood-rearing area, at lakes Klosterviken, Börringesjön and Yddingen, Scania, south Sweden, pooled over 1986-2002. All families having at least one neck collared parent were included. The number of young in each group is given above the columns.

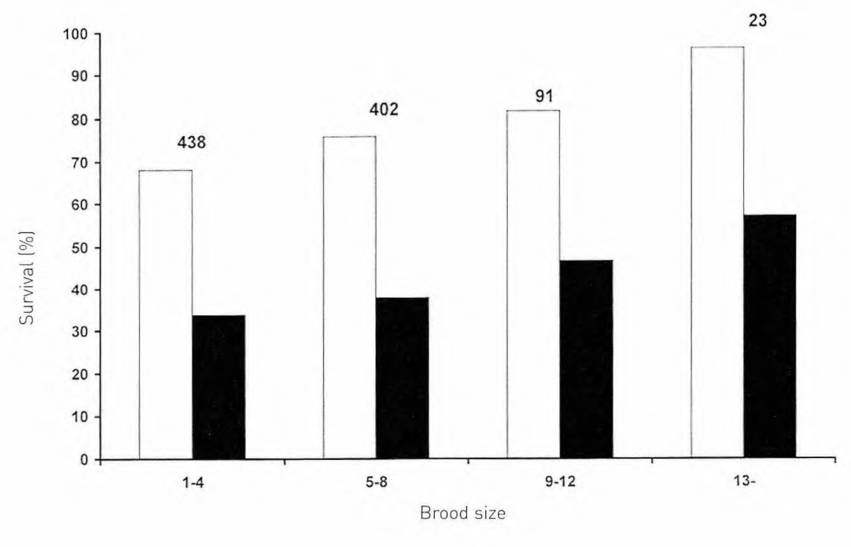

Figure 3. First year (light columns) and third year (dark columns) local survival (%) in relation to brood size at fledging of neck collared young fledged in the study area, Scania, south Sweden, in 1984-1998. Number of young in each group is given above the columns.

three years after fledging (ie normal earliest age at recruitment; Nilsson & Persson 1994), recruitment rate still correlated positively with family size (**Figure 5**), differences in recruitment rate being significant for all recruits (χ^2_3=7.92, P<0.05), whereas they were not significant for successful recruits (χ^2_3=7.27, n.s.).

Separate analyses of the different lakes showed a significantly higher rate of recruitment (all and successful recruits, respectively) with increasing family size for Lakes Yddingen (n=448; χ^2_3=13.85, P<0.01 and χ^2_3=14.35, P<0.01) and Klosterviken (n=291; χ^2_2=9.66, P<0.01 and χ^2_2=9.76, P<0.01), whereas no such correlation was found for Lakes Börringesjön (n=78; χ^2_1=0.08, n.s. and χ^2_1=0.41, n.s.) and Fjällfotasjön (n=77; χ^2_1=0.00, n.s. and χ^2_1=0.00, n.s.).

Parents in year t+1

Only one individual was seen with >12 young in more than one year: a female in Lake Börringesjön, with unmarked partner(s), fledged eight of 14 young in year t and 16 of 16 in year t+1, while data on fledging success were missing for year t+2.

Of adults that fledged 9-12 and >12 young respectively, in year t, 88% (n=34) and 82% (n=17) were alive during the following breeding season. Of 22 pairs that fledged 9-12 young in year t, 12 fledged 2-8 young and 10 failed in year t+1, while of eight pairs that fledged >12 young in year t, four fledged 2-5 young and four failed in year t+1.

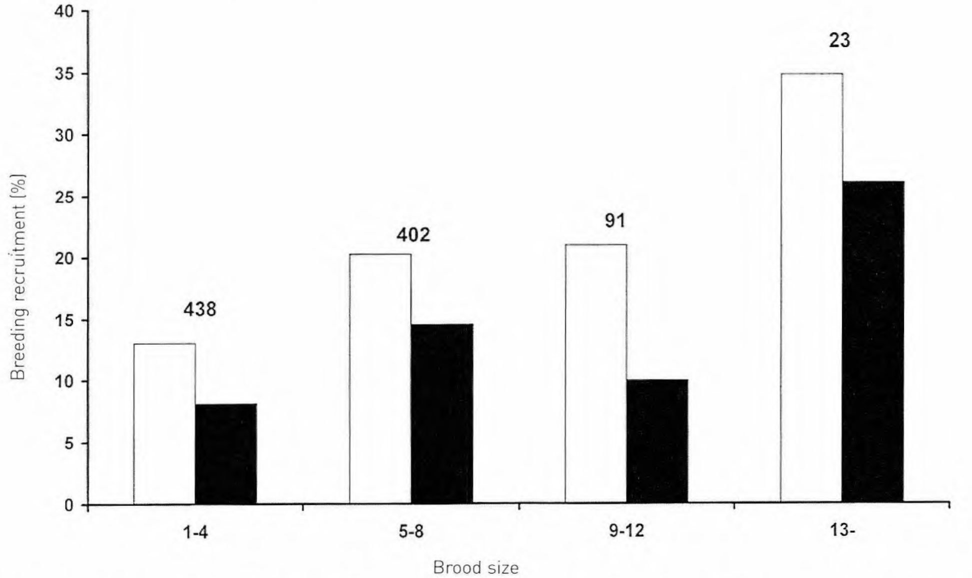

Figure 4. Breeding recruitment (%) in relation to brood size at fledging of neck collared young fledged in the study area, Scania, south Sweden, in 1984-1998. All (light columns) and successful (dark columns) recruits are shown. The number of young in each group given above the columns.

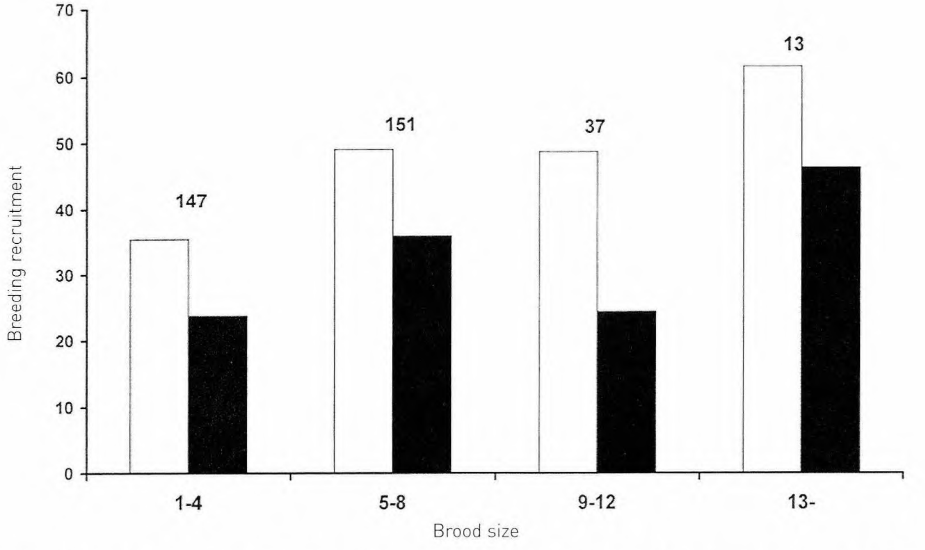

Figure 5. Breeding recruitment (%) in relation to brood size at fledging of neck collared young fledged in the study area, Scania, south Sweden, in 1984-1998 and surviving to the age of three. All (light columns) and successful (dark columns) recruits are shown. The number of young in each group given above the columns.

Discussion

Large broods may benefit in having faster gosling growth rates (Cooch *et al.* 1991; Lepage *et al.* 1998; Loonen *et al.* 1999) and higher dominance rank (Boyd 1953; Hanson 1953; Raveling 1970; Black & Owen 1989), allowing them to compete more successfully for and obtain better access to food resources (Gregoire & Ankney 1990), which consequently results in higher survival (Lepage *et al.* 1998; Loonen *et al.* 1999; Nilsson *et al.* 1997; this study) and recruitment probabilities (Nilsson *et al.* 1997; this study).

The pre-fledging survival estimate given in this study might have been inflated by an over-representation of young and inexperienced parents among the smallest brood sizes, such parents generally having a lower rearing success than experienced breeders (Raveling 1981; Zicus 1981; Rockwell *et al.* 1993; Nilsson 1998; but see Forslund & Larsson 1992). However, the exclusion of broods numbering 1-4 young when first seen in the rearing area does not change the outcome of the analysis.

In the present study, it was not possible to differentiate between within-pair and extra-pair young among the neck collared individuals. Thus, it was not possible to analyse whether there were any differences in survival and breeding recruitment between these two categories.

However, in studies of other goose species no significant differences were found between within-pair and extra-pair young, in either pre-fledging survival (Lank *et al.* 1990; Williams 1994), post-fledging survival (Lank *et al.* 1990; Larsson *et al.* 1995) or breeding recruitment (Lank *et al.* 1990; Larsson *et al.* 1995).

The fate of individual goslings between hatching and breeding recruitment could not be studied in this population, as all marking took place when goslings were 5-6 weeks old (Persson 1994). An indication of a gosling's probability of future breeding recruitment can be obtained, however, as soon as it arrives at the rearing area by combining **Figures 2 and 4**.

The fact that both pre- and post-fledging survival, as well as recruitment rate, showed a positive relationship with brood size ought to favour adoption in this population, provided there are no large costs to parents rearing additional young. The data in question for parents that fledged >12 young in year t were based, however, on small sample sizes and do not reveal any such costs. Survival between years t and t+1 (82%) was close to the long-term average of 83% (Nilsson & Persson 1993), and reproductive success in year t+1 (50% of pairs producing fledglings) equalled the long-term average, as 48% of all breeding attempts by experienced breeders resulted in at least one fledging (Nilsson & Persson 2001b). Adults that fledged 9-12 young in year t, on the other hand, had both a survival rate (88%) and a reproductive success (55%) that exceeded the long-term averages, which might be explained by their being 'better-quality' parents.

Published studies do not reveal any substantial cost to parents of rearing large broods, with or without extra-pair young. Even though feeding time was negatively correlated and the amount of vigilance positively correlated with brood size during brood-rearing, there was no relationship between number of goslings reared and probability of return or timing of breeding in the following year (Schindler & Lamprecht 1987; Forslund 1993; Williams *et al.* 1994; Loonen *et al.* 1999).

Available data clearly indicate that goose parents can enhance both the survival and breeding recruitment of their young by rearing extra-pair young, the more the better, which ought to make adoption a favoured breeding strategy. As this strategy is beneficial for the adults, it is surprising that it is not more commonly reported but, on the other hand, the opportunity to adopt is greatest in a dense breeding population and it is difficult to observe the different pairs when the population is unmarked.

The actual mechanism involved in gosling adoption is not clear. It is noted almost daily in the study population that some stray goslings are chased away while others are adopted, some adoptions involving goslings that are up to eight weeks old. These goslings are adopted at an age when both parents and offspring are capable of recognising each other (cf. also Choudhury *et al.* 1993; Williams 1994; Zicus 1981). A plausible explanation may be that "successful adults always adopt a gosling as long as it is not younger than and/or in an inferior physical condition to their own young". This seems to apply to the Scanian Greylag Goose, and very likely also to other goose populations. Support for this hypothesis comes from the fact that adopted goslings are nearly always impossible to single out from a mixed brood (authors' observations). To date, there have been no reports of geese 'stealing' young to increase the size of their own family, but it is possible given that a Greylag Goose pair in Utterslev Mose (Copenhagen, Denmark) reared 15, 41 and 35 young, respectively, in 1999, 2000 and 2001 (Henning Jensen, in litt.).

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References

Amat, J. 1987. Is nest parasitism among ducks advantageous to the host? *American Naturalist* 130: 454-457.

Andersson, M. & Åhlund, M. 2001. Protein fingerprinting: a new technique reveals extensive conspecific brood parasitism. *Ecology* 82: 1433-1442.

Beauchamp, G. 1997. Determinants of intraspecific brood amalgamation in waterfowl. *The Auk* 114: 11-21.

Black, J.M. & Owen, M. 1989. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Animal Behaviour* 37: 199-209.

Boyd, H. 1953. On encounters between wild White-fronted Geese in winter flocks. *Behaviour* 5: 85-129.

Brown, C.R. 1984. Laying eggs in a neighbour's nest: benefits and costs of colonial nesting in swallows. *Science* 224: 518-519.

Bustnes, J.O. & Erikstad, K.E. 1991. Parental care in the Common Eider *Somateria mollissima*: factors affecting abandonment and adoption of young. *Canadian Journal of Zoology* 69: 1538-1545.

Bustnes, J.O., Erikstad, K.E. & Bjørn, T.H. 2002. Body condition and brood abandonment in Common Eiders breeding in the High Arctic. *Waterbirds* 25: 63-66.

Choudhury, S., Jones, C.S., Black, J.M. & Prop, J. 1993. Adoption of young and intraspecific nest parasitism in Barnacle Geese. *Condor* 95: 860-868.

Cooch, E.G., Lank, D.B., Dzubin, A., Rockwell, R.F. & Cooke, F. 1991. Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rates. *Ecology* 72: 503-512.

Eadie, J.McA. & Lumsden, H.G. 1985. Is nest parasitism always deleterious to Goldeneyes? *American Naturalist* 126: 859-866.

Eadie, J.McA., Kehoe, F.P. & Nudds, T.D. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Canadian Journal of Zoology* 66: 1709-1721.

Forslund, P. 1993. Vigilance in relation to brood size and predator abundance in the Barnacle Goose, *Branta leucopsis*. *Animal Behaviour* 45: 965-973.

Forslund, P. & Larsson, K. 1992. Age-related reproductive success in the Barnacle Goose. *Journal of Animal Ecology* 61: 195-204.

Gregoire, P.E. & Ankney, C.D. 1990. Agonistic behaviour and dominance relationships among Lesser Snow Geese during winter and spring migration. *The Auk* 107: 550-560.

Hanson, H.C. 1953. Inter-family dominance in Canada Geese. *The Auk* 70: 11-16.

Hauff, P. 1982. Bestandsentwicklung und Brutbiologie der Graugans, *Anser anser*, im NSG Kuhlrader Moor and Röggeliner See. *Beiträge vor Vogelkunde* 28: 48-58.

Jensen, H. 2000. Ekstremt stort grågåsekuld *Anser anser*: Adoption eller ægdumpning af flere hunner? [In Danish with English summary: An extremely large brood of Greylag Goose *Anser anser*: Adoption or egg dumping by several females?] *Ornis Svecica* 10: 173-177.

Kampe-Persson, H. 2002. Greylag Goose *Anser anser*. *BWP Update* 4(3): 181-216.

Karlsson, J., Nilsson, L. & Persson, H. 1982. Grågåsen som häckfågel i Skåne 1978-1982. [In Swedish with English summary: Breeding of the Greylag Goose *Anser anser* in Skåne, South Sweden, 1978-1982.] *Anser* 21: 223-232.

Kilpi, M., Öst, M., Lindström, K. & Rita, H. 2001. Female characteristics and parental care mode in the crèching system of Eiders, *Somateria mollissima*. *Animal Behaviour* 62: 527-534.

Lank, D.B., Cooch, E.G., Rockwell, R.F. & Cooke, F. 1989. Environmental and demographic correlates of intraspecific nest parasitism in Lesser Snow Geese *Chen caerulescens caerulescens*. *Journal of Animal Ecology* 58: 29-45.

Lank, D.B., Rockwell, R.F. & Cooke, F. 1990. Frequency-dependent fitness consequences of intraspecific nest parasitism in Snow Geese. *Evolution* 44: 1436-1453.

Larsson, K., Tegelström, H. & Forslund, P. 1995. Intraspecific nest parasitism and adoption of young in the Barnacle Goose: effects on survival and reproductive performance. *Animal Behaviour* 50: 1349-1360.

Lazarus, J. & Inglis, I.R. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. *Animal Behaviour* 34: 1791-1804.

Lepage, D., Gauthier, G. & Desrochers, A. 1998. Larger clutch size increases fledging success and offspring quality in a precocial species. *Journal of Animal Ecology* 67: 210-216.

Loonen, M.J.J.E., Bruinzeel, L.W., Black, J.M. & Drent, R.H. 1999. The benefit of large broods in Barnacle Geese: a study using natural and experimental manipulations. *Journal of Animal Ecology* 68: 753-768.

Nilsson, L. 1998. The Greylag Goose *Anser anser* as a model species for the study of waterfowl breeding ecology. *Acta Zoologica Lituanica, Ornithologia* 8: 20-28.

Nilsson, L. & Persson, H. 1992. Feeding areas and local movement patterns of post-breeding Greylag Geese *Anser anser* in South Sweden. *Ornis Svecica* 2: 77-90.

Nilsson, L. & Persson, H. 1993. Variation in survival in an increasing population of the Greylag Goose *Anser anser* in Scania, southern Sweden. *Ornis Svecica* 3: 137-146.

Nilsson, L. & Persson, H. 1994. Factors affecting the breeding performance of a marked Greylag Goose *Anser anser* population in south Sweden. *Wildfowl* 45, 33-48.

Nilsson, L. & Persson, H. 2001a. Natal and breeding dispersal in the Baltic Greylag Goose *Anser anser. Wildfowl* 52: 21-30.

Nilsson, L. & Persson, H. 2001b. Change of mate in a Greylag Goose *Anser anser* population: effects of timing on reproductive success. *Wildfowl* 52: 31-40.

Nilsson, L., Green, M. & Persson, H. 2002. Field choice in spring and breeding performance of Greylag Geese *Anser anser* in south Sweden. *Wildfowl* 53: 7-25.

Nilsson, L., Persson, H. & Voslamber, B. 1997. Factors affecting survival of young Greylag Geese *Anser anser* and their recruitment into the breeding population. *Wildfowl* 48: 72-87.

Persson, H. 1994. Halsringmärkning av grågäss *Anser anser* i Skåne 1984-1993. [In Swedish with English summary: Neck-banding of Greylag Geese *Anser anser* in Scania, 1984-1993.] *Anser* 33: 101-106.

Persson, H. 1997. Den vitkindade gåsens *Branta leucopsis* etablering i Skåne. [In Swedish with English summary: Breeding of the Barnacle Goose *Branta leucopsis* in Skåne, 1986-1996.] *Anser* 36: 11-15.

Persson, H. 2000a. Halsringmärkning av grågäss i Skåne 1984-2000. [In Swedish with English summary: Neck collaring of Greylag Geese *Anser anser* in Scania, 1984-2000.] *Anser* 39: 167-172.

Persson, H. 2000b. Neck collar retention in a Greylag Goose *Anser anser* population. *Ornis Svecica* 10: 155-160.

Persson, H. 2002. Kullsammanslagning hos grågås *Anser anser*. [In Swedish with English summary: Brood amalgamation in the Greylag Goose *Anser anser*.] *Ornis Svecica* 12: 96-99.

Pöysä, H. 1995. Factors affecting abandonment and adoption of young in Common Eiders and other waterfowl: a comment. *Canadian Journal of Zoology* 73: 1575-1577.

Raveling, D.G. 1970. Dominance relationships and agonistic behaviour of Canada Geese in winter. *Behaviour* 37: 291-319.

Raveling, D.G. 1981. Survival, experience, and age in relation to breeding success of Canada Geese. *Journal of Wildlife Management* 45: 817-829.

Rockwell, R.F., Cooch, E.G., Thompson, C.B. & Cooke, F. 1993. Age and reproductive success in female Lesser Snow Geese: experience, senescence and the cost of philopatry. *Journal of Animal Ecology* 62: 323-333.

Schindler, M. & Lamprecht, J. 1987. Increase of parental effort with brood size in a nidifugous bird. *The Auk* 104: 688-693.

Warhurst, R.A. & Bookhout, T.A. 1983. Effect of gang-brooding on survival of Canada Goose goslings. *Journal of Wildlife Management* 47: 1119-1124.

Weigmann, C. & Lamprecht, J. 1991. Intraspecific nest parasitism in Bar-headed Geese *Anser indicus*. *Animal Behaviour* 41: 677-688.

Williams, T.D. 1994. Adoption in a precocial species, the Lesser Snow Goose: intergenerational conflict, altruism or a mutually beneficial strategy? *Animal Behaviour* 47: 101-107.

Williams, T.D., Loonen, M.J.J.E. & Cooke, F. 1994. Fitness consequences of parental behaviour in relation to offspring number in a precocial species: the Lesser Snow Goose. *The Auk* 111: 563-572.

Witkowski, J. 1983. Population studies of the Greylag Goose *Anser anser* breeding in the Barycz valley, Poland. *Acta Ornithologica* 19: 179-216.

Zicus, M.C. 1981. Canada Goose brood behaviour and survival estimates at Crex Meadows, Wisconsin. *Wilson Bulletin* 93: 207-217.