

Cooperation, Conflict, and Crèching Behavior in Goldeneye Ducks

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abstract: Crèching behavior, or brood amalgamation, results in offspring being reared by adults other than their genetic parents. Although a variety of hypotheses have been proposed to explain this behavior, most assume either that brood amalgamation is accidental (i.e., nonselected) or that adoption of young is selected for because of social benefits to the young and/or adopting parents. We propose, instead, that brood amalgamation is a function of two separate processes: brood desertion and brood adoption. To examine brood desertion, we develop a graphic model to predict when parents should abandon their young and we test this model experimentally for the Barrow's goldeneye (*Bucephala islandica*). As predicted, females deserted their offspring when the size of the brood was experimentally reduced. Brood adoption occurred when deserted ducklings joined other broods. However, the success of ducklings in doing so was strongly dependent on the availability of potential host broods and on the age of the recipient broods. Foreign ducklings were readily accepted into young broods (<10 d old) but invariably were rejected from old broods. We could detect no benefits or costs of brood adoption to the host females, contrary to the expectations of a social benefit hypothesis. Our experiments indicate that crèching behavior is driven by selection on adults to abandon their brood when the benefits of continued investment are outweighed by the reduction in future reproduction and selection on deserted ducklings to join other broods to obtain parental care. Rather than a form of cooperative brood care, crèching in goldeneyes is perhaps best considered as a form of reproductive parasitism, entailing parent-offspring conflict over brood desertion and intergenerational conflict over adoption of abandoned young.

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Kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971), or mutualism are often invoked to explain the origin and maintenance of cooperative behavior among individuals. On closer examination, however, many putatively cooperative behaviors turn out to be driven more by conflict than by cooperation (see, e.g., Brockmann 1984; Brown 1987). Crèching behavior, or brood amalgamation, provides a classic example of an apparently cooperative behavior—young from different broods/families combine into a single group and subsequently receive care from parents other than their own (reviews in Riedman 1982; Eadie et al. 1988). This behavior has been recorded in a variety of organisms, including fishes (McKaye 1981; Wisendon and Keenleyside 1992), mammals (Riedman 1982), and birds (esp. the Anatidae; Eadie et al. 1988). However, despite the widespread occurrence of crèching behavior in diverse taxonomic groups, it is still unclear why parents accept and care for young that are not their own. Until recently, crèching has been studied almost exclusively from the perspective of social benefits to donors and/or recipients, the underlying assumption being that adoption of young is the behavior under selection (McKaye 1981; Eadie et al. 1988; Wisendon and Keenleyside 1992). An opposing view is that crèching is simply a nonselected consequence of intense intraspecific aggression and territoriality (Savard 1987). The debate has thus been polarized into two extremes: one favoring direct, indirect, or reciprocated benefits to donors and recipients, and the other arguing that crèching is a non-adaptive epiphenomenon.

We develop an alternative interpretation—specifically, that crèching is driven first by parental investment decisions of the “donor” parent, such that parents abandon young when it is no longer profitable to continue to provide care. Amalgamation of broods may then be a sec-

ondary outcome of selection acting on deserted offspring to find another brood to join. There may be no net benefit, either direct or indirect, present or future, to the adopting parent; indeed, there may be selection acting on parents to prevent the adoption of unrelated offspring. As such, crèching may be viewed best as a consequence of intergenerational conflict between adults and offspring (Pierotti 1991), rather than a form of cooperative brood care or an inadvertent consequence of intraspecific aggression. While similar views have been suggested by previous authors (e.g., Bustnes and Erikstad 1991), there has yet to be a direct attempt to uncouple the processes underlying brood desertion and brood adoption. We do so here for a cavity-nesting sea duck, the Barrow's goldeneye (*Bucephala islandica*).

We focus first on brood desertion and ask why parents abandon their offspring. We develop a graphic model, based on parental investment theory, to determine when it would be profitable for a parent to desert its brood, and we test this model experimentally in a field study of Barrow's goldeneyes in British Columbia. Experimental studies of brood desertion are rare (Carlisle 1985; Armstrong and Robertson 1988; Winkler 1991) but are essential to control for extraneous factors that might influence parental investment decisions. We then consider brood adoption and investigate the factors that dictate whether abandoned offspring will successfully become integrated into another brood. Finally, we examine some of the costs and benefits of desertion/adoption to each participant to determine whether the interactions among individuals are cooperative or competitive. Our results indicate that apparently cooperative behaviors, such as brood adoption, may be understood more fully by considering the ecological constraints on parental care and by examining potential conflicts of interest among parents and their offspring.

Defining the Desertion Threshold

We begin by making three fundamental assumptions for organisms with precocial young. First, we assume that the number of offspring that survive is a positive and linear function of brood size and that this is a reasonable measure of fitness (fig. 1A). Second, we assume that parental care results in higher survivorship of young. Thus, broods with a parent in attendance produce more offspring (top line in fig. 1A) than broods without care (bottom line in fig. 1A). The net benefit of care (the difference between these two lines) therefore increases as brood size increases (i.e., the two lines diverge). Finally, we assume that there is some cost to providing care to young. In the short term this may be time, energy, or mortality risk, but ultimately it is calculated as the num-

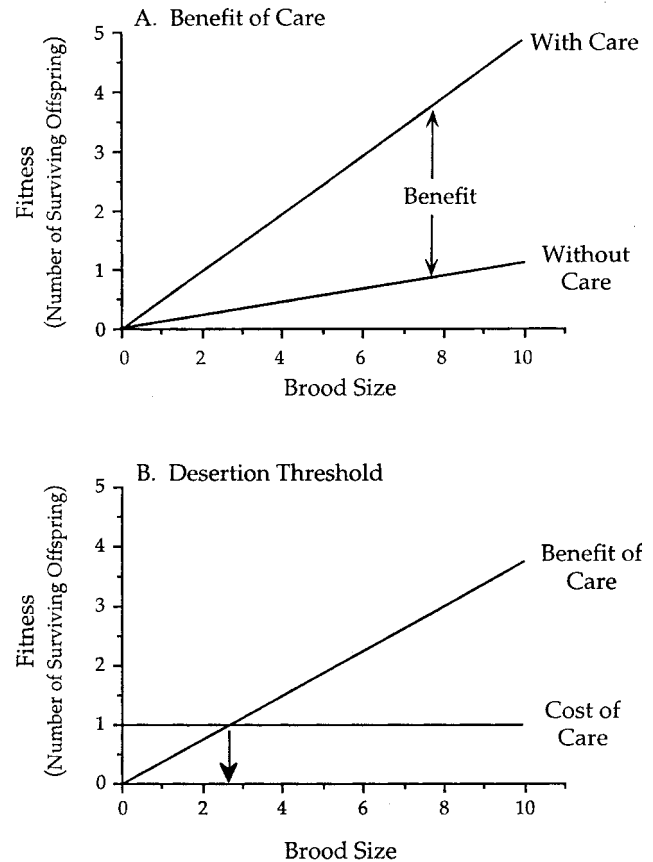


Figure 1: The desertion threshold model predicts the brood size at which parents should desert their brood. A, Net benefit of parental care as the difference between the survivorship of young with care (*upper line*) and without care (*lower line*). B, Benefit and cost curves are combined and define the brood size (*arrow*) below which parents should abandon their young. The cost and benefit functions illustrated are hypothetical.

ber of future offspring that could have been produced had the parent abandoned the present brood. We assume that this cost does not increase with brood size (i.e., care is shareable *sensu* Wittenberger 1981), although the model applies whenever the slope of the cost function is lower than the benefit function and the two lines intersect.

Combining the costs and benefits of staying with the present brood reveals a hypothetical brood size threshold at which the costs of staying equal the benefits (fig. 1B). This brood size defines the desertion threshold, below which parents should abandon their current brood in favor of future reproductive opportunities. As long as there is some benefit to parental care and as long as the provision of this care leads to a reduction in residual reproductive value, there will necessarily be some threshold brood size below which brood abandonment is favored. This concept is not new (e.g., see Tait 1980; Wickler and

Seibt 1983; Taborsky 1985; Mock and Parker 1986; Armstrong and Robertson 1988; Winkler 1991; Pöysä 1992; Pöysä et al. 1997). However, our model provides an explicit representation of the trade-offs that were implicit in earlier studies of brood desertion.

We next test this model with Barrow's goldeneyes, a cavity-nesting sea duck. As with most parental investment models, it is difficult or impossible to determine empirically the costs and benefits of parental care in the same currency (i.e., the functions in fig. 1); consequently, we could not predict precisely the brood size at which desertion should occur. We therefore tested the model by experimentally reducing the size of goldeneye broods and predicted that the frequency of brood desertion should increase as brood size is reduced and there should be a threshold brood size below which desertion is predominant.

Methods

Study Species

Barrow's goldeneyes are medium-sized sea ducks (Anatidae, Tribe Mergini) restricted to the west coast of North America and Iceland. As secondary cavity nesters, goldeneyes readily use artificial nest structures; most of the birds in this study nested in wooden nest boxes. Pairs arrive on the breeding area in early April, and nesting begins within a week of arrival, continuing until the beginning of June. Males defend a site-specific territory during the egg-laying period (Savard 1988) but play no role in incubation or brood care and desert the females during the first week of incubation. Females typically lay clutches of seven to 10 eggs over a 2-wk period and then incubate the clutch for approximately 30 d. The precocial young leave the nest within 24–48 h of hatching and are able to feed and swim on their own as soon as they leave the nest. The female guards the brood for up to 4–8 wk, aggressively defending a brood territory. The ducklings fledge at approximately 60 d of age.

Brood desertion and adoption (crèching) occur frequently in Barrow's goldeneye (Savard 1987; see "Results"). On occasion, we have witnessed aggressive interactions among females resulting in one female abandoning her young to another female (see also Savard 1987). In other cases, we have observed ducklings alone and apparently deserted, and later found some of these young adopted into another brood. Most observations, however, comprise a sighting of a female attending her brood, and then several days later, the female is observed without a brood while her young are found in a crèche attended by a different female. Similar patterns of brood desertion and adoption have been reported for the congeneric common goldeneye (*Bucephala clangula*; Palmer

1975; Pöysä 1992; Eadie et al. 1995; Pöysä et al. 1997). The difficulty in clearly separating the effects of desertion and adoption using only observational data led us to undertake the experiments reported here.

Study Area

This study was conducted in the Cariboo parklands of British Columbia, Canada. The focus of this study is a set of experiments conducted in 1986; for comparison, we also draw on information collected in an observational study conducted from 1984 to 1992 (J. McA. Eadie, unpublished data). The study area encompassed 28 ponds (1–30 ha) and lakes (40–120 ha) on two sites: the 108 Mile House area, near the village of 100 Mile House, and the 148 Mile House area, near the town of William's Lake. All of the lakes and ponds were permanent, alkaline, and relatively shallow (usually less than 3 m) with little emergent vegetation other than bulrush (*Scirpus acutus*) and cattail (*Typha latifolia*).

Field Methods

Nest boxes and suitable natural cavities were censused every 4–7 d to find active nests. Once located, nests were visited every day or two on most lakes. Females were trapped on the nest during the third week of incubation and were then weighed, measured (culmen, wing, and tarsus length), and banded with numbered metal leg bands and color-coded leg bands. Most females were also fitted with color-coded nasal saddles (Doty and Greenwood 1974) to permit identification of individuals from a distance. Upon hatching, all ducklings were weighed, measured, and web-tagged using monel fingerling tags (Haramis and Nice 1980). Newly hatched ducklings were marked on one or both cheek patches with colored permanent-ink pens, and each brood received a unique color combination. This enabled us to determine broods of origin for ducklings that were deserted and/or adopted.

Brood Reduction Experiment

Observational analyses of brood desertion may be confounded by the effects of female age or quality, territory quality, or seasonal variation. To test the desertion threshold model presented in figure 1, we experimentally manipulated broods of 12 females by removing ducklings within 24 h after hatching, before the broods left the nest. Broods of 14 other females in the same study area were maintained as controls. Broods were assigned randomly to experimental and control treatments and were exposed to equal levels of handling, marking, and visits

to the nest prior to brood exodus. Some of the broods in our experiment had been parasitized by conspecifics during egg laying. We did not manipulate the brood sizes in these nests because it would have required the removal of a large number of ducklings. To control for possible effects of parasitism on our experiment, we repeated all analyses excluding broods with more than 10 ducklings (i.e., parasitized broods). The results did not differ between these analyses, and so we present the results of the analyses using all broods. Six of the 14 control broods were also used in the duckling addition experiments (see below). Since our hypothesis was effectively one-tailed (i.e., reduced broods should be more likely to be deserted), addition of ducklings should not affect the test. However, to be conservative, we repeated our analyses excluding these broods.

Preliminary observations of natural broods suggested that females may be more likely to desert young broods with less than five ducklings. Accordingly, we reduced the 12 experimental broods to an average size of 3.5 ± 0.2 ducklings (one brood of two ducklings, five broods of three ducklings, five broods of four ducklings, and one brood of five ducklings). This was significantly smaller than the size of control broods (brood size at hatching of the 14 control broods: 9.6 ± 0.8 ducklings; Mann-Whitney test, $z = 4.33$, $P < .001$). Ducklings that were removed from nests were maintained in captivity until we were able to place them into other broods (see below).

After ducklings left the nest boxes we monitored the fates of the ducklings and classified each female into three response categories: female stayed with the brood, female deserted the brood, and the brood disappeared. We also determined whether ducklings from deserted broods were adopted into other broods. Broods classified as having "disappeared" were those where the entire brood completely vanished and none of the ducklings were ever seen alone or adopted into host broods. We could not be certain that these broods had not been deserted first and then suffered total brood mortality or, alternatively, were deserted by their mother in secluded areas with dense vegetation, where the likelihood of subsequent observation of untended ducklings would be low. The latter fate was known to have occurred for one deserted brood. Given the uncertainty of the actual fates of "disappeared broods," we analyzed female responses both including and excluding these broods.

To examine the effect of host availability (number of potential host broods) on the adoption of deserted ducklings, we monitored the location and abundance of all other broods on the same study lake as our experimental broods. A brood was considered to be a potential host only if it was less than 10 d old—females with older broods did not accept foreign young (see the "Results" section).

We examined the effect of brood size on desertion in 40 unmanipulated broods for which we had reliable measures of the number of young and information on fate of the brood (deserted or not; an additional nine broods disappeared, and we could not determine their fate with certainty). Mortality of goldeneye young is highest in the first week after hatch, resulting in variable reductions in the size of broods. Because the observational broods were not experimentally manipulated, we used the number of young censused immediately prior to the date of desertion, rather than the number of young at hatch, as the relevant measure of brood size for deserted ducklings. To provide an appropriate comparison for nondeserted broods, we used the brood size from the nearest comparable census (approx. 1 wk of age; range = 1–7 d).

Duckling Addition Experiments

We added ducklings to 14 broods to examine the factors that influence whether ducklings are adopted and the consequences of adoption to duckling survival. Ducklings were obtained from the brood reduction experiments (above). From one to five ducklings, each 1–3 d old, were added to each experimental brood (one duckling added to each of six broods; two ducklings added to three broods, three ducklings added to two broods, four ducklings to one brood, and five ducklings to two broods). All recipient broods hatched 1–21 d prior to the experiment; females had established brood territories. In all but three cases, we added ducklings at a single time to the experimental brood. In the remaining three cases, we added ducklings twice, once when the recipient female had a young brood (1, 2, and 8 d old) and a second time 2–13 d later (14, 4, and 21 d of age, respectively). We released ducklings at the edge of ponds, near the territory of the recipient female. We considered only cases where there was some interaction between the duckling and host brood or female (i.e., approach, calling). Typically, ducklings vocalized frequently, and females reacted quickly to their presence. In some cases (see "Results") females became aggressive to the added ducklings. Because of this response, we limited the number of brood additions, precluding collection of larger samples sizes. In situations where added ducklings were rejected by host females, we recaptured the duckling and placed it in a receptive brood off the study area.

Duckling Survival

We censused broods every 3–4 d to monitor duckling survival. Young were considered to have survived if still alive on day 21 (very little mortality occurs after this point; Savard et al. 1991). Most broods were monitored for a much longer period (range 25–54 d; average

34.5 d). We calculated brood survival using two methods. First, we determined the proportion of young that survived from each brood. Because we had complete histories of broods and ducklings (i.e., from hatching to the 21-d survival cutoff), this direct measure of brood survival was unlikely to have been affected by bias introduced by variation in sampling intensity or by missing observations. Second, we repeated our analyses using a measure of survival based on a modified Mayfield estimate (see Savard et al. 1991). For each interval between censuses, we determined duckling exposure as the number of days multiplied by the number of ducklings in the brood. The daily mortality rate was then calculated for each brood as the number of ducklings lost divided by the number of ducklings-days of exposure. The daily survival rate is simply $(1 - \text{daily mortality rate})$, and a measure of total survival for the brood can be calculated as s^n , where s is the daily survival rate and n is the total number of days the brood was observed.

We repeated all analyses of duckling survival using the direct measure of survival (proportion of brood surviving to 21 d), the Mayfield estimate of daily survival rate, and the Mayfield estimate of total survival (s^n). All of these measures were significantly correlated ($r^2 = 0.67\text{--}0.97$, all $P < .001$). Moreover, analyses based on different measures of survival did not differ either in the pattern observed or in statistical significance. Accordingly, we present the analyses based on the direct measure of brood survival (proportion surviving) because of its simplicity and the ease with which it can be compared to other species. Duckling survival tended to be negatively related to hatch date (proportion surviving, $r^2 = 0.12$, $N = 30$, $P = .063$; daily survival rate, $r^2 = 0.10$, $P = .084$), although the decline was not significant. To ensure that season did not affect our results, we repeated all analyses of duckling survival using residuals from regressions of survival on hatching date. These results also did not differ from those based on uncorrected values.

Duckling survival was analyzed in relation to the following categories: broods where the female stayed ("with female") versus deserted broods ("deserted"); deserted broods that were adopted by another female ("adopted") versus deserted broods that remained untended by any female ("alone"); and broods of females that adopted young ("host") versus broods where young were not adopted ("with mother"). Only natural adoptions were included in the analysis of deserted broods. However, experimental adoptions were included when assessing consequences of adoption to host broods or postadoption survival of adopted ducklings. We compared survival of all adopted ducklings with all other ducklings tended by their mothers. We also used a matched pair comparison (adopted young vs. host young within host broods) to control for potential variation in female and territory

quality. When assessing the effect of brood size on duckling survival, brood size of a host female includes her own young plus adopted young, although we focus on the survival of the host young.

Throughout, all statistical probabilities are two-tailed. Tests of independence were conducted using log-likelihood ratios (G tests), with William's correction for continuity. Two-sample comparisons were analyzed by Mann-Whitney tests after correcting for tied observations. Correlations between variables were examined using Spearman-rank correlation coefficients. We report means and standard errors in the text.

Results

Desertion of Ducklings: Testing the Desertion Threshold Model

Reductions in brood size had a strong and significant effect on female parental care responses. Considering first only broods of known fate ("female stays" or "brood is deserted"), control and reduced broods differed significantly in brood fate ($G = 4.40$, $P < .05$; table 1). The pattern was even stronger when we combined the categories "abandoned" and "disappeared" under the rationale that "disappeared" broods may have been deserted prior to disappearing ($G = 7.42$, $df = 1$, $P < .01$). Finally, if we exclude the six control broods that were used in the brood addition experiments, the pattern is unchanged ($G = 5.76$, $df = 1$, $P < .02$). Desertion of broods typically occurred within a few days of hatching (mean: 2.62 d, range: 1–4 d, $N = 8$).

Pooling over all experimental treatments, the threshold brood size for desertion is between four and six ducklings (fig. 2). The average size of broods that were deserted was 4.1 ± 0.6 ducklings ($N = 10$) compared to 8.5 ± 0.9 ducklings ($N = 16$) in broods where the female remained (Mann-Whitney $z = 3.22$, $P < .002$).

We compared these results to patterns of naturally occurring desertion. Of 49 unmanipulated Barrow's goldeneye broods followed on our study area, eight were deserted. An additional nine broods disappeared immediately after hatching, but we could not determine whether these broods suffered total mortality or were

Table 1: The effects of experimental brood reduction on brood abandonment by Barrow's goldeneye females

	Fate of brood		
	Female stayed	Abandoned	Disappeared
Control	12	1	1
Reduced	4	4	4

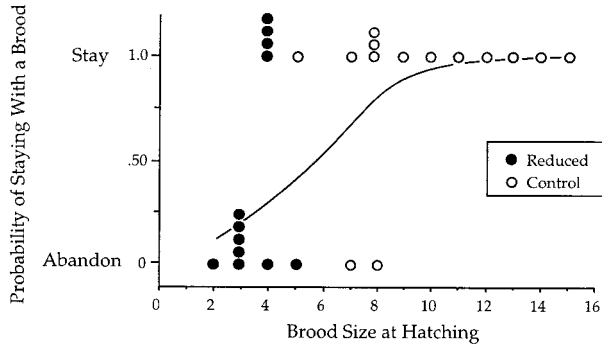


Figure 2: The effect of experimental reductions of brood size on brood desertion by Barrow's goldeneyes. The line indicates the logistic regression between the manipulated brood size and the probability that a female would remain with her brood. The equation is: $p(\text{stay}) = \exp(-2.71 + 0.55 \times \text{brood size}) / (1 + \exp(-2.71 + 0.55 \times \text{brood size}))$; likelihood ratio $\chi^2 = 11.15$, $N = 26$, $P < .001$.

first deserted and subsequently perished. Thus, between 16% (eight of 49) and 34% (17 of 49) of broods were deserted. Deserted broods were significantly smaller (3.0 ± 0.3 ducklings, $N = 8$) than nondeserted broods of comparable age (8.0 ± 0.5 ducklings, $N = 32$, $z = 3.95$, $P < .001$; fig. 3; broods of uncertain fate were excluded from this and further analyses). The desertion threshold in unmanipulated broods appeared to be approximately four ducklings (fig. 3). The size of deserted broods did not differ between the experimental and observational studies (Mann-Whitney $z = 1.10$, $P = .26$) and the logistic re-

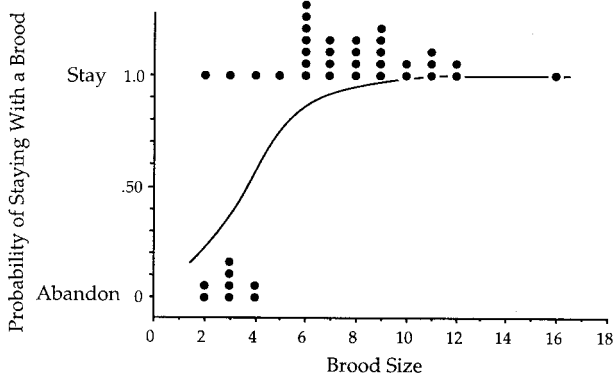


Figure 3: The relationship between brood size and desertion in unmanipulated broods of Barrow's goldeneyes. The line indicates the logistic regression between brood size and the probability that a female would remain with her brood. The equation is: $p(\text{stay}) = \exp(-2.75 + 0.76 \times \text{brood size}) / (1 + \exp(-2.75 + 0.76 \times \text{brood size}))$; likelihood ratio $\chi^2 = 24.10$, $N = 40$, $P < .001$.

gressions indicated a similar pattern of desertion in response to brood reductions (cf. figs. 2 and 3).

We examined other factors for our experimental broods that might influence whether females deserted or stayed with their offspring. There were no detectable differences in hatching date ($P = .41$), female breeding experience/age ($P = .46$), or hatching success (proportion of eggs that hatched; $P = .53$) between females that deserted ($N = 10$) and those that stayed with their offspring ($N = 16$). Likewise, there was no influence of host availability (i.e., nearby broods that could act as recipients of abandoned young) on the frequency of brood desertion ($G = 0.91$, $df = 2$, $P > .50$).

Adoption of Ducklings

Frequency of Adoption. Ducklings from three of the 10 deserted experimental broods were subsequently adopted into another brood (one was with a bufflehead brood). This indicates that brood amalgamation can result from the behavior of offspring after they are abandoned and suggests that crèche formation is linked with brood desertion, particularly of small broods. Similar rates of adoption were observed in natural broods. Young from eight of 49 unmanipulated broods (16%) were adopted into other broods, while 11 females (22%) accepted foreign offspring (young from a single brood were occasionally adopted into more than one host brood). In both the experimental and observational studies, all crèches were attended by only a single female.

Host availability (numbers of potential recipient broods) influenced whether deserted ducklings were adopted successfully. For the 10 deserted broods from the experimental study, the average number of potential hosts was significantly higher for broods that were adopted (2.7 ± 0.3 , $N = 3$) than for broods that remained on their own (0.7 ± 0.3 , $N = 7$; Mann-Whitney $z = 2.35$, $P = .019$). There were no differences between the adopted and nonadopted broods in several other variables examined (number of ducklings that hatched, $P = .58$; brood size after reduction, $P = .18$; proportion of eggs hatched, $P = .70$; number of young removed, $P = .91$; or age of young when deserted, $P = .99$).

Duckling Addition Experiments. Host rejection had a large effect on whether abandoned offspring were accepted by another female. Of the 14 experiments in which we added ducklings to broods attended by a female, host females accepted foreign young in six cases (43%) and rejected the young in eight cases (57%). Rejections were not passive. Most females reacted by chasing the duckling away from the brood, but some females pursued the foreign duckling to the point of leaving their own brood un-

Costs and Benefits of Desertion or Adoption

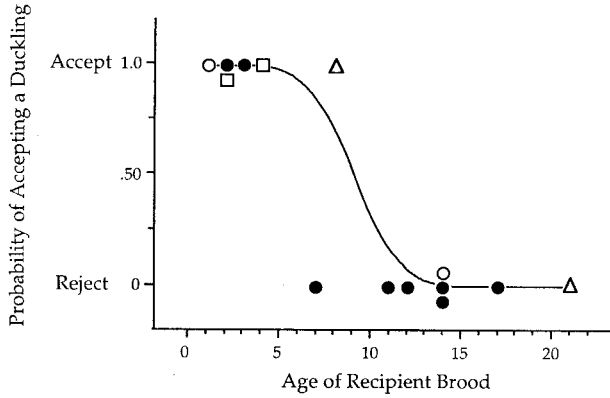


Figure 4: The effect of brood age (days) on the probability that experimentally added ducklings (1–2 d old) would be accepted into a recipient brood. The line indicates the logistic regression between brood age and the probability that a female would accept a foreign duckling. Open symbols indicate three females that were tested twice; each female is represented by a different symbol. The equation is: $p(\text{accept}) = \exp(6.721 - 0.894 \times \text{age}) / (1 + \exp(6.721 - 0.894 \times \text{age}))$; likelihood ratio $\chi^2 = 15.06$, $N = 14$, $P < .001$.

attended. In two cases, the female killed the foreign young before we could intervene. Rejection of ducklings was clearly due to aggression by the potential host female, not a lack of interest by the duckling in joining the new brood.

Age of the host brood had a critical influence on whether newly hatched ducklings were adopted into another brood (fig. 4). The average age of host broods in the six cases where ducklings were accepted was 3.3 ± 1.0 d compared with an average age of 13.8 ± 1.5 d for the eight cases where ducklings were rejected (Mann-Whitney $z = 2.99$, $P < .003$). Categorical analysis indicates that the age of the host ducklings was a robust predictor of whether a day-old duckling would be accepted (fig. 4); five of six females accepted foreign ducklings when their broods were <10 d old, whereas all five females with broods >10 d rejected foreign young ($G = 8.56$, $df = 1$, $P < .01$).

We were able to retest three females that had accepted added ducklings when their brood was young (<10 d) to determine whether the response to foreign young changed within an individual female as her brood aged (see *open symbols*, fig. 4). One female was retested when her brood was still <10 d old—she accepted; the other two females were retested when their broods were >10 d and both rejected. This sample is too small to test statistically, but it suggests that the response of females changes with age and that the 10-d threshold holds within, as well as among, females.

Consequences of Desertion. Ducklings that were deserted had significantly lower survival than ducklings in broods with their mother in our experimental broods (fig. 5A; proportion of young fledging in deserted broods: 0.16 ± 0.09 , $N = 7$ deserted broods alone + 2 deserted broods that were adopted; broods with the female: 0.62 ± 0.05 , $N = 6$ host broods + 9 broods with mother; Mann-Whitney $z = 3.16$, $P < .002$). Identical patterns were found using a Mayfield daily survival estimate (deserted broods: 0.59 ± 0.13 , broods with the female: 0.98 ± 0.01 , $z = 3.14$, $P < .002$). Deserted ducklings also suffered higher mortality than young with a female in unmanipulated broods (proportion of young fledging in deserted broods: 0.28 ± 0.05 , $N = 8$; broods with the

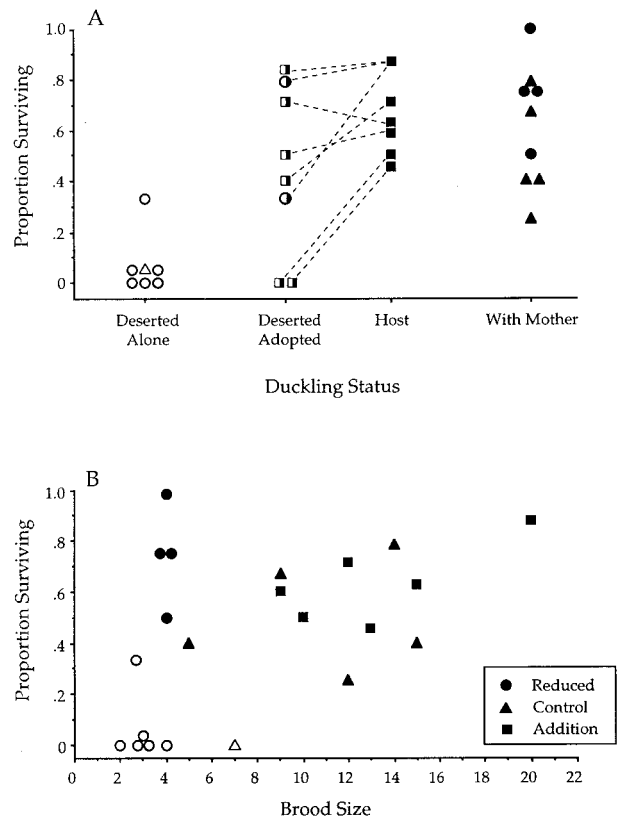


Figure 5: Survival of Barrow's goldeneye ducklings (proportion of young surviving to more than 21 d) as a function of (A) duckling status and (B) brood size in an experimental study. Symbols indicate the experimental treatment (*circle* = brood reduced, *triangle* = control, *square* = ducklings added). Broods that were deserted are indicated by open symbols, adopted broods are indicated by half-filled symbols, and broods that remained with their mother are indicated by filled symbols.

female: 0.66 ± 0.04 , $N = 32$; Mann-Whitney $z = 3.64$, $P < .001$). Correcting for hatching date did not alter any of these patterns, nor did excluding broods that “disappeared” (rather than were clearly “deserted”).

Deserted ducklings include both those that were subsequently adopted and those that remained alone. When analyzed separately, the survival of ducklings that were not adopted (“alone”) was significantly lower than the survival of adopted ducklings (fig. 5A; proportion fledging, alone: 0.05 ± 0.05 , $N = 7$; adopted: 0.45 ± 0.12 , $N = 2$ natural adoptions + 6 experimental adoptions; Mann-Whitney $z = 2.45$, $P < .02$). The survival of adopted ducklings did not differ significantly from that of ducklings remaining with their mother (0.62 ± 0.05 , $N = 6$ “host” broods + 9 broods “with mother”; fig. 5A; Mann-Whitney $z = 1.07$, $P = .28$). Because the latter analysis potentially confounds differences among females or brood territories, we conducted a paired comparison of the survival of adopted young versus host young in the same brood (dashed lines connect broods in fig. 5A). In this analysis, adopted young experienced lower survival than ducklings of the host female (Wilcoxon matched-pairs test, $z = 2.10$, $P = .036$, $N = 8$ comparisons). None of these patterns were changed when we controlled for hatching date or when we used Mayfield estimates of survival.

Consequences of Adoption. We examined the consequences of adoption to host (recipient) broods using two approaches: we compared duckling survival in broods where females adopted young (“host”) to those where ducklings were not adopted (“with mother”; fig. 5A); and we analyzed duckling survival as a function of brood size, since adoption results in larger broods (fig. 5B). There was no difference in fledging success between females that adopted offspring (0.57 ± 0.07 , $N = 6$) and females that did not adopt young (0.61 ± 0.08 , $N = 9$; Mann-Whitney $z = 0.42$, $P = .68$). The result did not change when we repeated the analysis by examining only the survival of the host female’s own ducklings (Mann-Whitney $z = 0.06$, $P = .95$).

Considering all 22 experimental broods, fledging success increased with brood size (fig. 5B; $r_s = 0.50$, $P < .03$; after correcting for hatching date, $r_s = 0.42$, $P = .058$). However, this result was entirely a consequence of the very low survival of deserted broods (*open symbols*, fig. 5B). When these broods were excluded from the analysis, there was no relation between brood size and survival ($r_s = -0.13$, $P = .64$; correcting for hatching date, $r_s = -0.26$, $P = .34$). In fact, the correlation becomes negative, opposite to that expected if survival is enhanced in large broods.

Discussion

Brood Desertion, Offspring Adoption, and Crèching

Traditionally, explanations for crèching behavior, or brood amalgamation, have focused on two mutually exclusive hypotheses: crèching is an adaptive behavior, driven primarily by the reduced risk of predation in large, pooled broods of ducklings (Munro and Bédard 1977; Eadie et al. 1988); or crèching is a nonadaptive outcome of accidental brood mixing during encounters between families (Savard 1987). Our study presents a third alternative—specifically, that brood desertion is the primary target of selection, with subsequent adoption of offspring (crèching) occurring as a secondary consequence. This is not a novel idea—other authors have reported that brood desertion occurs in waterfowl (Pöysä 1992; Pöysä et al. 1997) and may be an important factor leading to brood amalgamation, particularly for females under energetic stress (Gorman and Milne 1972; Bustnes and Erikstad 1991). However, in most studies, the focus was on the potential cooperative nature of the crèche—indeed, the English translation of “crèche” means nursery, implying a communal or cooperative system of brood care. Females were presumed to abandon their young to a crèche, thereby obtaining care for young while also being freed to meet other metabolic or nutritional demands (Gorman and Milne 1972; Bustnes and Erikstad 1991). The difficulty with these explanations is that they fail to separate the relative contributions of two independent processes underlying crèche formation: brood desertion and brood adoption. Desertion and adoption may be so strongly coupled in many species that it would be virtually impossible to disentangle the causes and consequences of one from the other without experimental studies.

Our study allowed us to uncouple these processes. We first developed a parental investment model to illustrate why it might be adaptive for females to desert their current brood. Based on the assumption that there is a cost of parental care (fig. 1B), we predicted that there would be a brood size below which females should desert their brood (the desertion threshold). Our experimental results provide strong support for this prediction (fig. 2). By reducing brood sizes at hatching, we lowered the expected benefits to females of providing care, and, as predicted, females deserted these low value broods. The striking similarity between the patterns of brood desertion in the experimental and observational studies indicates that our experiment successfully replicated a natural phenomenon. Moreover, brood value (present and prospective) has recently been implicated as a factor affecting brood desertion in common goldeneyes (*Bucephala clangula*; Pöysä 1992; Pöysä et al. 1997). Our study is dis-

tinguished by the fact that some of our deserted experimental broods, and many of the observational broods, ended up in crèches, providing evidence for a direct link between brood desertion and crèching in goldeneyes.

We emphasize that the goal of our brood reduction experiment was not to demonstrate directly a cost of parental care for goldeneyes but, rather, to test the prediction that abandonment would be dependent on brood size. Our experiments therefore provide indirect evidence that desertion is beneficial to females. However, the inference is that there is a cost of reproduction for goldeneyes—why else would females abandon their current brood? A second line of evidence further supports this notion. Survival of ducklings, once deserted, was significantly reduced relative to broods remaining with a female (fig. 5). That females would desert their young, in spite of the reduction in current reproductive success by doing so, implies that females do indeed balance the value of continued investment in their current brood against the prospects for survival and future reproduction. The manner by which females are able to make these assessments and adjustments is unknown but represents a fruitful area for further research.

Our results lead us to reject the hypothesis that crèching is due to nonadaptive, accidental brood mixing (Savard 1987). The strong associations found between brood size and the occurrence of desertion and crèching in goldeneyes are not predicted by the accidental mixing hypothesis. In effect, the accidental brood-mixing hypothesis makes no specific predictions and, as such, represents a null hypothesis. The fact that we found nonrandom patterns of desertion and adoption—and did so in an experimental study that controlled for potentially confounding effects of female quality, territorial quality, and seasonality—indicates that brood desertion and crèching in goldeneyes are not simply accidental events.

We also found no evidence that crèche formation in Barrow's goldeneyes is driven by the benefits to ducklings of living in large broods. Although adoption improved the survival of ducklings once they had been deserted, adoption into a crèche did not improve the survival of ducklings over what could have been expected had they been raised by their own mother. Likewise, there was no functional relationship between duckling mortality and brood size—ducklings did not survive better in larger broods, as hypothesized by previous authors (Andersson 1984; Eadie and Lumsden 1985; Eadie et al. 1988; Kehoe 1989; but see Milonoff et al. 1995). Our comparison of duckling survival and brood size did, however, indicate that spurious patterns may arise if one fails to uncouple the separate influences of adoption and desertion on duckling survival. When we first examined the relation between brood size and offspring survival, we found that

survival was higher in larger broods. However, this pattern was generated entirely by the effects of desertion—small broods were more likely to be deserted, and desertion significantly reduced offspring survival. When deserted broods were removed from the analysis, the positive relationship between brood size and survival not only disappeared, but the trend became slightly negative as well. Clearly, any attempt to explore the functional relationship between brood size and survival (e.g., Andersson and Eriksson 1982; Milonoff et al. 1995), or the adaptive basis of crèching behavior, requires careful partitioning of the separate effects of desertion and adoption.

A surprising result of our study was the strong aggression shown by potential host females toward ducklings seeking adoption. Although this aggression suggests that hosts incur costs by adopting young, our attempts to measure these costs directly failed to indicate what they might be. Neither a comparison of females who adopted and those who did not nor a comparison of the relation between brood size and duckling survival revealed any evidence for a cost of adoption. This leaves us with three possibilities: adoption is not costly to host females; the costs are indirect; or costs and benefits of adoption vary with the age of the brood. The first possibility seems unlikely given the marked aggression of hosts, to the point where they left their own broods unattended to chase foreign ducklings. The second explanation is plausible given that there are at least two indirect costs that our study would have been unable to detect: adoption may lead to reduced female survival or reduced future reproduction if larger broods require more parental effort than smaller ones do (Røskaft 1985) or adoption might interfere with a female's ability to monitor her own brood size and make appropriate parental investment decisions. If females are unable to discriminate adopted offspring from their own offspring, adoption would result in some total brood sizes being above the desertion threshold whereas, in actuality, the number of the female's own young is below the threshold.

The third possibility, that the costs or benefits of adoption vary with the age of the brood, is interesting given that potential hosts were not uniformly aggressive toward all foreign ducklings. Females that accepted foreign ducklings had similar-sized young ducklings of their own, while females that rejected foreign offspring had larger, older ducklings. A simple explanation for this pattern is that females require more than 10 d to learn to recognize their own ducklings. However, it is also possible that adoption of additional young is beneficial early in the brood-rearing period as a buffer against predation when mortality is highest, but detrimental later in the brood-rearing period when competition among ducklings for

food or other resources might be most intense. Adoption of small, recently hatched ducklings might also be costly for females with older broods if younger ducklings slow the brood down during movements between feeding areas or extend the period of total time the female remains with the brood before independence.

The Nature of Crèching: Cooperation or Conflict?

The reproductive and survival strategies of adult and young goldeneyes combine to produce a remarkably diverse social system, involving interactions among several participants, each with their own self-interests. Understanding the relative roles of cooperation or conflict in such a social system ultimately depends on being able to evaluate the independent fitness consequences of adoption and desertion to each participant. Our analysis of the costs and benefits of crèching behavior in goldeneyes suggests that it entails at least three separate conflicts of interest (table 2).

First, deserting female goldeneyes and their abandoned offspring are caught in a parent-offspring conflict (Trivers 1974). Desertion is always detrimental to ducklings, yet beneficial to females if their brood sizes fall below the desertion threshold. Females appear to have the upper hand in this conflict, simply because ducklings cannot physically force their mothers to stay and tend them. However, deserted young have the option of attempting to join other broods, leading to a second conflict of interest. Deserted ducklings clearly benefit from adoption, while the aggressive behavior of potential host females suggests that they incur a cost if they adopt foreign young. The resolution of this intergenerational conflict (Pierotti 1991) apparently has a strong age-dependent

component (ducklings are accepted up until 10 d of age). We cannot yet determine whether ducklings win this conflict during the first week because of learning constraints in females (the time required to recognize offspring) or whether the conflict only develops after a brood is >10 d old.

A third conflict of interest arises between the adult females. Deserting females gain through adoption (because their deserted ducklings fare better when adopted than if left on their own) whereas adoption is potentially costly to hosts. The interaction between adult females is probably best considered a form of reproductive parasitism rather than the mutualistic, cooperative relationship once envisaged (e.g., review in Eadie et al. 1988). The question to be answered now is whether this is direct parasitism, whereby deserting females facilitate adoption of their ducklings into crèches, or an indirect form of parasitism mediated entirely through the behavior of the deserted ducklings.

One final interaction, that between adopted ducklings and those in the host brood, deserves mention. Previous analyses of crèching behavior have largely ignored the role of ducklings, yet ducklings are in a position to influence significantly their mother's desertion tendencies. For example, ducklings might facilitate adoption of other offspring into the brood and, as a result, reduce the chance that the total brood size will drop below the desertion threshold. Adoption does not appear to be costly to host young, and ducklings may share common interests in maintaining large brood sizes. Perhaps the reason that broods amalgamate so readily during brood encounters (Savard 1987) is because ducklings are strongly attracted to each other. Strong attraction among ducklings would make sense, given that their own mothers may eventually desert them and that potential host females may attempt to kill them. Viewed in this light, the only truly cooperative element of crèching behavior in goldeneyes may be the interactions that occur among host and adopted ducklings.

Table 2: Consequences to the participants involved in brood desertion and adoption in Barrow's goldeneyes

<i>Participant</i>	<i>Observed costs or benefits of</i>	
	<i>Desertion</i>	<i>Adoption</i>
Deserted ducklings	–	+
Deserting females	(+)	+
Host ducklings	N/A	0
Host females	N/A	(–)

Note: A plus sign indicates that the participant receives a benefit, a minus sign indicates a cost, "0" indicates a neutral effect, N/A indicates that the cost or benefit was not applicable to that participant, and parentheses denote cases where the effect was inferred from behavioral responses rather than assessed with a direct measure of costs and benefits. Desertion does not affect hosts directly, but indirectly through its influence on adoption.

Conclusion

Much progress has been made in the last several decades in understanding the complex dynamics underlying animal social systems. Behaviors that once were thought to be altruistic or mutualistic have, on closer examination, often revealed a far more complex web of conflict and cooperation. Crèching behavior in goldeneyes fits well within this emerging view. We cannot yet determine whether the patterns observed in our study are typical of most, or even many, species of waterfowl. Indeed, the variation in crèching behavior observed among the

Anatidae (e.g., M. Williams 1974; Munro and Bedard 1977; Boos et al. 1989; Kehoe 1989; T. D. Williams 1994) indicates a richness to this social system that remains to be explored. Progress in these efforts will be accomplished more rapidly by uncoupling the fundamental processes underlying this behavior—brood desertion and adoption. Only by doing so, can we clearly evaluate the potential conflicts of interest among participants and thereby develop a more predictive theory on how such conflicts are likely to be resolved.

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Literature Cited

- Andersson, M. 1984. Brood parasitism within species. Pages 195–228 in C. J. Barnard, ed. *Producers and scroungers: strategies for exploitation and parasitism*. Croon Helm, London.
- Andersson, M., and M. O. G. Eriksson. 1982. Nest parasitism in goldeneyes *Bucephala clangula*: some evolutionary aspects. *American Naturalist* 120:1–16.
- Armstrong, T., and R. J. Robertson. 1988. Parental investment based on clutch value: nest desertion in response to partial clutch reduction in dabbling ducks. *Animal Behaviour* 36:941–943.
- Boos, J. D., T. D. Nudds, and K. Sjöberg. 1989. Posthatch brood amalgamation by mallards. *Wilson Bulletin* 101: 503–505.
- Brockmann, H. J. 1984. The evolution of social behavior in insects. Pages 340–361 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology*. 2d ed. Sinauer, Sunderland, Mass.
- Brown, J. L. 1987. *Helping and communal breeding in birds*. Princeton University Press, Princeton, N.J.
- Bustnes, J. O., and K. E. Erikstad. 1991. Parental care in the common eider (*Somateria mollissima*): factors affecting abandonment and adoption of young. *Canadian Journal of Zoology* 69:1538–1545.
- Carlisle, T. R. 1985. Parental response to brood size in a cichlid fish. *Animal Behaviour* 33:234–238.
- Doty, H. A., and R. J. Greenwood. 1974. Improved nasal saddle marker for mallards. *Journal of Wildlife Management* 38:938–939.
- Eadie, J. McA., and H. G. Lumsden. 1985. Is nest parasitism always deleterious to goldeneyes? *American Naturalist* 126:859–866.
- Eadie, J. McA., F. P. Kehoe, and T. D. Nudds. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Canadian Journal of Zoology* 66:1709–1721.
- Eadie, J. McA., M. L. Mallory, and H. G. Lumsden. 1995. Common goldeneye: *Bucephala clangula*. The birds of North America, ed. A. Poole and F. Gill, No. 170. Academy of Natural Sciences, Philadelphia; and American Ornithologists' Union, Washington, D.C.
- Gorman, M. L., and H. Milne. 1972. Crèche behaviour in the common eider *Somateria m. mollissima* L. *Ornis Scandinavica* 3:21–25.
- Hamilton, W. D. 1964. The genetical theory of social behaviour, I, II. *Journal of Theoretical Biology* 7:1–52.
- Haramis, G. M., and A. D. Nice. 1980. An improved web-tagging technique for waterfowl. *Journal of Wildlife Management* 44:898–899.
- Kehoe, F. P. 1989. The adaptive significance of crèching behaviour in the white-winged scoter (*Melanitta fusca deglandi*). *Canadian Journal of Zoology* 67:406–411.
- McKaye, K. R. 1981. Natural selection and the evolution of interspecific brood care in fishes. Pages 173–183 in R. D. Alexander and D. W. Tinkle, eds. *Natural selection and social behavior*. Chiron, New York.
- Milonoff, M., H. Pöysä, and J. Virtanen. 1995. Brood-size-dependent offspring mortality in common goldeneyes reconsidered: fact or artifact? *American Naturalist* 146:967–974.
- Mock, D. W., and G. A. Parker. 1986. Advantages and disadvantages of egret and heron brood reduction. *Evolution* 40:459–470.
- Munro, J., and J. Bédard. 1977. Gull predation and crèching behaviour in the common eider. *Journal of Animal Ecology* 46:799–810.
- Palmer, R. S. 1975. Common goldeneye: *Bucephala clangula* (Bonaparte). Pages 373–399 in R. S. Palmer, ed. *Handbook of North American birds*. Vol. 3. Waterfowl (pt. 2). Yale University Press, New Haven, Conn.
- Pierotti, R. 1991. Infanticide versus adoption: an intergen-

- erational conflict. *American Naturalist* 138:1140–1158.
- Pöysä, H. 1992. Variation in parental care of common goldeneye (*Bucephala clangula*) females. *Behaviour* 123:247–260.
- Pöysä, H., J. Virtanen, and M. Milonoff. 1997. Common goldeneyes adjust maternal effort in relation to prior brood success and not current brood size. *Behavioral Ecology and Sociobiology* 40:101–106.
- Riedman, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology* 57:405–435.
- Røskoft, E. 1985. The effect of enlarged brood size on the future reproductive potential of the rook. *Journal of Animal Ecology* 54:255–260.
- Savard, J.-P. L. 1987. Causes and functions of brood amalgamation in Barrow's goldeneye and bufflehead. *Canadian Journal of Zoology* 65:1548–1553.
- . 1988. Winter, spring and summer territoriality in Barrow's goldeneye: characteristics and benefits. *Ornis Scandinavica* 19:119–128.
- Savard, J.-P. L., G. E. J. Smith, and J. N. M. Smith. 1991. Duckling mortality in Barrow's goldeneye and bufflehead broods. *Auk* 108:568–577.
- Taborsky, M. 1985. On optimal parental care. *Zeitschrift für Tierpsychologie* 70:331–336.
- Tait, D. E. N. 1980. Abandonment as a reproductive tactic—the example of grizzly bears. *American Naturalist* 115:800–808.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.
- . 1974. Parent-offspring conflict. *American Zoologist* 14:249–269.
- Wickler, W., and U. Seibt. 1983. Optimal maternal care. *Zeitschrift für Tierpsychologie* 63:201–205.
- Williams, M. 1974. Crèching behaviour of the Shelduck *Tadorna tadorna*. *Ornis Scandinavica* 5:131–143.
- Williams, T. D. 1994. Adoption in a precocial species, the lesser snow goose: intergenerational conflict, altruism or mutually beneficial strategy? *Animal Behaviour* 47:101–107.
- Winkler, D. W. 1991. Parental investment decision rules in tree swallows: parental defense, abandonment, and the so-called Concorde Fallacy. *Behavioral Ecology* 2:133–142.
- Wisendon, B. D., and M. H. A. Keenleyside. 1992. Intra-specific brood adoption in convict cichlids: a mutual benefit. *Behavioural Ecology and Sociobiology* 31:263–269.
- Wittenberger, J. F. 1981. *Animal social behavior*. Duxbury, Boston.

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