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ORIGINAL ARTICLE

Benefits of large broods by higher chick survival and better territories in a precocial shorebird

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Abstract When reproductive success is constant in one breeding phase, different tactics that increase variation in reproductive success among individuals may evolve in other phases. For instance, in shorebirds, which usually have a limited clutch size of four eggs, variation in reproductive tactics among individuals is expected either before egg-laying (e.g. diverse mating systems) or after hatching of the young (e.g. diverse parental care). In this paper, I studied the pied avocet (*Recurvirostra avosetta*), a shorebird with a modal clutch size of four eggs, to test whether post-hatch chick adoption as an alternative tactic can be linked to increased variation in annual reproductive success. When predation was high, naturally adopting pairs produced more filial fledglings than did pairs not adopting chicks and not losing chicks to adoption. The number of filial fledglings increased with the number of adopted young, possibly through diluting the chances of predation on filial young. Experimental chick addition did not lead to more fledged young due to low brood integrity as shown by the frequent loss of chicks from some experimental broods. When predation was low, larger broods occupied feeding territories with higher prey abundance than smaller broods, possibly due to their dominance over smaller ones. Pairs that lost chicks to adoption (donors) fledged as many filial young in their broods as did non-adopters/non-donors, whereas the total number of donors' filial fledglings, including those raised in adopting broods, approached that of adopters. These findings show, for the first time, that post-hatch alternative reproductive tactics can lead to variation in annual reproductive success and to higher success for some pairs even in species where past adaptations limit variation in reproductive success in a certain phase of reproduction.

Keywords Alloparental care · Brood manipulation · Dilution effect · Optimal clutch size · Territory quality

Introduction

Natural selection favours individuals which maximize their lifetime reproductive success. Life history theory, however, suggests that clutch or litter size is limited by a trade-off between current reproductive effort and future fitness (Stearns 1992). In birds and mammals, this trade-off is influenced by the ability of parents to produce eggs/young or to provision the young (Godfray et al. 1991; VanderWerf 1992; Sikes 1998), imposing physiological or energetic costs that limit optimal clutch or litter size below the maximum size possible (Stearns 1992; Monaghan and Nager 1997).

In shorebirds (suborder Charadrii), clutch size is limited by the energetic and physiological costs of producing a clutch that is larger relative to body size than in other birds and/or by the costs of incubating extra eggs (Hills 1980; Winkler and Walters 1983; Shipley 1984; Delehanty and Oring 1993; Székely et al. 1994; Yogev et al. 1996; Sandercock 1997; Arnold 1999; Larsen et al. 2003; Hanssen et al. 2005). The costs of brood-rearing, however, are probably small for such birds because adults in most shorebirds do not feed their young, and parental care is non-depreciable and unshared, i.e. benefits each young

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equally (Lazarus and Inglis 1986; Lessells 1986; Monaghan and Nager 1997; but see Walters 1982; Dzus and Clark 1997; Milonoff et al. 2004).

When variation in reproductive success related to clutch size per se is limited among individuals, alternative reproductive tactics resulting in greater variation in reproductive success may be favoured by selection in other phases of reproduction. Shorebirds are expected to show such variation in reproductive tactics before or after the incubation phase because the maximum clutch size in most species is four eggs (MacLean 1972). One such tactic for birds with precocial young is to increase the size of the brood after hatching either through adoption of non-filial young, crèching or brood amalgamation. These forms of alloparental care are frequent in birds with precocial young (e.g. Riedman 1982; Pierotti and Murphy 1987; Eadie et al. 1988; Cooper and Miller 1992; Lanctot et al. 1995; Beauchamp 1997; Pöysa and Milonoff 1999; Lengyel 2002), and some of these tactics can lead to higher adult fitness and/or chick survival. For example, brood size and social dominance are positively related in several goose and duck species, which often translates in larger broods accessing better resources than smaller broods (brood-dominance hypothesis; Raveling 1970; Lazarus and Inglis 1978; Black and Owen 1989a; Kehoe 1989; Williams 1994; Lepage et al. 1998; Öst and Kilpi 2000). In barnacle geese (*Branta leucopsis* Bechstein), experimental evidence shows that enlarged broods are dominant and occupy better feeding territories than controls, especially when intraspecific competition for territories is high (Loonen et al. 1999). A larger brood may also lead to decreased per capita predation rates for young (dilution-of-predation hypothesis; Hamilton 1971). For example, overall mortality due to predation decreases with brood size in common eiders (*Somateria mollissima* L.; Munro and Bedard 1977) and in white-winged scoters (*Melanitta fusca deglandi* L.; Kehoe 1989). Other post-fledging benefits associated with large broods include higher dominance on the wintering grounds, increased overwinter survival of adults, larger clutch size the following year and higher number of young wintering the following year (Black and Owen 1989b; Petersen 1992; Williams 1994).

By using field observations and brood manipulations, I tested the dilution-of-predation and brood-dominance hypotheses in the pied avocet (*Recurvirostra avosetta* L.), a shorebird with a modal clutch size of four eggs, fully precocial young and frequent adoption of non-filial young. I measured the fledging success of young in natural and manipulated broods in low-predation and high-predation areas. I then compared which component of the variation in brood size (number of young hatched, naturally adopted or lost, experimentally added or removed) is related to fledging success in both areas to evaluate the dilution-of-predation effect. I predicted that brood size increase due to natural adoption and/or experimental addition of chicks will increase fledging success of filial young in high-predation areas more than in low-predation areas. To test the brood-dominance hypothesis, I quantified territory quality by the abundance of potential prey items in brood feeding territories. If pairs with larger broods are dominant over those with smaller ones, pairs with larger broods can occupy territories of higher prey abundance. Thus, I predicted that prey abundance on the territory will be positively related to the size of the brood occupying it. Finally, if larger broods provide either of the above benefits, pairs that increase the size of their brood by adopting alien chicks are expected to reap such benefits. I specifically predicted that pairs which adopt non-filial chicks will fledge more of their own filial young than will pairs which do not adopt non-filial chicks. In addition, I also tested whether the survival of adopted chicks increases by adoption, or whether adoption is related to the quality of the parents.

Materials and Methods

Pied avocets were studied in Kiskunság National Park in south-central Hungary near Fülöpszállás village (46°48′N, 19°10′E) between 1998 and 2000. The study area (112 km^2) includes several alkaline lakes (natural habitats of avocets), a fishpond and a reconstructed wetland (man-made or semi-natural habitats). Avocets nest in colonies, mostly on small islands, and lay a clutch of four eggs. Pairs may renest if their first clutch fails early in the season but produce only one brood per year. Avocets are socially monogamous, and both parents care for the young, which move and feed on their own soon after hatching (Cramp and Simmons 1983). Details on the breeding biology of avocets at the study sites are given elsewhere (Lengyel 2006).

Nesting colonies (n=21) were found visually; all nests (n=257, all in colonies) were marked, and clutch size was recorded. Egg length and breadth were measured and egg volume was estimated as in Hoyt (1979). The stage of incubation and the expected date of hatching (±1 day) were estimated using the egg-flotation method (Nol and Blokpoel 1983; Alberico 1995). Colonies with nests at hatching were searched for young chicks in early mornings when chicks were usually warmed in the nest-cup by their parents. Chicks were considered to belong to the nest in which they were found and were covered with a cloth to keep them warm and to prevent them from leaving the nest while researchers were handling other nests. Young (<24-h-old) chicks were marked individually by two color-rings and a piece of tape attached on the metal ring. No eggs or chicks were harmed in this study, nor did color rings cause injury or death to chicks. Culmen length, tarso-metatarsus length and body mass were measured for most chicks, and chick body size was estimated by factor scores obtained by a principal component analysis of these variables.

I monitored avocet broods near the colony, on brood-leading routes and in brood-rearing areas at regular intervals (2–3 days) from a car or hunting blinds and recorded the location of territories and the composition of avocet broods on maps. A chick was considered fledged if it was seen after age 35 days (Cramp and Simmons 1983) and was considered dead if it was not seen on three or more consecutive observations. Resighting probability was high due to the sparse vegetation and the isolation of the study sites by agricultural fields, e.g. only two broods (0.5% of n=367 broods hatching at the sites) were known to fledge without being resighted.

The size of avocet broods typically changed after hatching, but before the broods departed from the colony. Brood size changed in the colony for 34% of the broods (n=257 broods with known composition). The size of some broods increased by chick adoption, and that of others decreased by chick loss to adoption or chick death by natural reasons (predation or adverse weather). Adoptions were inferred from resighting observations. Chick adoptions were recorded when a non-filial chick was seen integrated in a family other than the natal brood at least twice during brood-rearing. Adopted chicks (n=92 total) were observed in 53 broods (21% of n=257), resulting an average of 1.7+(SD) 1.16 adopted chicks (range 1–6) per brood. Most (86%) chicks were adopted in the colony, and adoptions occurred in all but one colony where young hatched from ten or more clutches (n=12 colonies). Adults did not behave aggressively toward the young (<1-week-old) alien chicks and always accepted them. A more detailed account on chick adoption is given elsewhere (Lengyel 2002).

Brood size in this study refers to the number of chicks when the brood departed from the nesting colony, i.e. after chick adoptions took place. Pairs with young left the nesting colonies 1–2 days after hatching and moved to feeding areas where parents defended territories from other adults. Based on differences in predation pressure and predation-related variation in space use by avocet broods (Lengyel 2006), the study sites were categorized into either low-predation areas (natural habitats: three alkaline lakes, n=16 colonies) or high-predation areas (semi-natural sites: one fishpond, one wetland, n=5 colonies). In low-predation areas, pairs led their young from the island colonies to the shore and occupied territories on the shore of their natal lake. In contrast, more than half of the pairs hatching young in high-predation areas left the natal lake with their broods due to a shortage of chick feeding territories, intense territorial aggression among pairs and frequent visits by predators. All such pairs attempted to move their young to nearby low-predation areas (alkaline lakes), but only 18% of the broods (n=100) were observed to reach such areas (Lengyel 2006). Treks through land masses involved high mortality for chicks because they were exposed to both land and aerial predators and had to tackle physical obstacles (e.g. motorway, reed beds, canals and arable lands) and considerable distances (at least 1 km but up to 4 km). As a result, many chicks perished before 10 days of age, but mortality after this age was rare. The proportion of broods that produced at least one fledgling was significantly higher (68%) for pairs hatching young in low-predation areas (n=66 in 1998–1999) than for pairs doing so in high-predation ones (30%, n=126; Lengyel 2006). More details on habitat-related differences in breeding success are given in Lengyel (2006).

To test the effect of brood size on chick survival to fledging, I manipulated the composition and size of newly hatched broods in both high-predation areas and low-predation areas in 1999. Experimental units were avocet broods, and each brood and chick was used only once. When at least three clutches were hatching simultaneously within a colony, broods were randomly allocated into one of four treatment levels: (1) enlarged broods: one alien chick was added to the brood (enlargement treatment, n=26 broods), (2) modified broods: one alien chick was added to the brood and a filial chick was removed from the brood (adoption treatment and enlargement control, n=24), (3) reduced broods: one filial chick was removed from the brood (brood reduction treatment, n=15) and (4) control broods: no chick was added to or removed from the brood, but chicks were handled in the same way as in other groups (double control, n=26). Chicks to be added or removed were selected at random. After selecting experimental chicks and broods, chicks were transferred to the target nest and placed in the nest-cup, which also contained at least one hatching egg or newly hatched young. The source and target broods always were the same age (<2-day-old). Adults did not show aggression towards experimental chicks, and each experimental chick was seen as part of the target brood at least once. Experimental broods had equal numbers of hatched young ($F_{3,87}$=1.324, p=0.272), whereas brood size differed after the manipulation and before broods departed from the colony (Table 1, $F_{3,87}$= 26.680, p<0.0001). Experimental broods did not differ from each other or from non-experimental broods in either egg-laying or hatching date, clutch size or egg size and chick body size (generalized linear mixed-effects models using natal colony nested within natal lake as random factor to control for non-independent origin of broods; egg-laying date $F_{1,235}$=0.427, p=0.514; hatching date $F_{1,235}$=0.761, p=0.384; clutch size $F_{1,235}$=2.514, p=0.114; egg volume

Table 1 Size and number of pied avocet broods used in this study by experimental treatment and by whether the pair adopted chicks, lost chicks to adoption or to natural reasons or the brood remained unchanged after the manipulation took place at the nest, but before broods left the nesting colonies usually 1 to 2 days post-hatch

		Number of broods				
Experimental group	Number of chicks after manipulation[a]	Adopting chick(s)	Losing chick(s)	Adopting and losing chicks	Unchanged	Total
Enlarged (+1 chick)	4.3±0.75 (2–5)	8	1	1	16	26
Modified (+1/−1 chick)	3.4±0.65 (2–4)	1	6	4	13	24
Reduced (−1 chick)	2.2±0.86 (1–3)	2	4	1	8	15
Control (±0 chick)	3.4±0.75 (2–4)	0	5	0	21	26
Non-experimental	2.9±1.02 (1–5)	9	29	17	111	166
	Total	20	45	23	169	257

Data on experimental groups are from eight colonies in 1999, whereas the "non-experimental" group also contains data from 13 other colonies in 1998–2000.

[a] Mean±SD (range)

$F_{1,135}=0.300$, $p=0.588$, chick body size averaged per brood $F_{1,189}=0.181$, $p=0.671$).

To quantify territory quality, I estimated the abundance of potential prey items available to chicks on the feeding territories. Potential prey included macroscopic invertebrates (waterbugs *Heteroptera*: *Corixidae*, *Notonectidae* and *Gerridae*, larval dragonflies *Odonata*, water beetles *Coleoptera*: *Dytiscidae* and *Gyrinidae*, chironomids *Chironomidae* and annelid worms *Oligochaeta*). Sampling was conducted only on the first territory of young (<2 weeks) broods and only if the territory was occupied by the same brood for more than 3 days. Potential prey were sampled by collecting all invertebrates from the water enclosed by a plastic cylinder (diameter 45 cm) placed in the center of the territory, where water depth varied between 2 and 13 cm. I then used a small sweepnet (diameter 15 cm, mesh size 0.2 mm) to collect invertebrates from the water, with also mixing up lake sediments but without scraping the hard bottom of the lake. Prey were not sampled in high-predation areas where territories often shifted due to intraspecific aggression and disturbance by predators. The number of prey items per liter water was log-transformed to stabilize variances.

Data on 257 broods originating from 20 colonies on five lakes/ponds are used in this study. To control for the non-independence of broods due to colonial nesting, I applied generalized linear mixed-effects (GLME) models with 'natal colony' nested within 'lake/pond' as a random block factor (R statistical environment, function 'lme'). GLME models use an iterative process based on restricted maximum-likelihood, can incorporate nested random effects while allowing the within-group errors to be correlated and/or have unequal variances and are robust to unbalanced designs (R Development Core Team 2004). The number of filial young fledged per brood was the response variable in most analyses. Survival probabilities were not used because the number of fledglings was known for each brood and was considered a better measure of reproductive success than pre-fledging chick survival.

Many broods, including experimental ones, changed by natural chick adoption or loss before leaving the nesting colony (Table 1). To evaluate the relative importance of such changes on the number of fledglings, brood size at the departure from the colony was partitioned into five components (number of chicks hatched, experimentally added, experimentally removed, naturally adopted and naturally lost), which were entered simultaneously as independent variables in GLME models. The random effect of 'colony-nested-within-lake/pond' was not influential (intercept SD < residual SD) in any of the models presented. Pseudoreplication due to the presence of more than one brood by the same individual in the 3 years was unlikely because only one (4%) of the marked adults ($n=25$) bred in more than one year (with a failed nest in the first of 2 years), and the flux of individuals between Hungarian and coastal populations (unpublished data) and frequent clutch failure (50%) further decreased the chance that broods from the same individual are included. The number of fledglings per brood did not differ by year (GLME models, $p>0.09$), therefore, data from the 3 years were pooled. Mean values were adjusted for hatching date when necessary. Means±SDs are reported except where indicated, and two-tailed probabilities ($\alpha=0.05$) were used.

Results

Relationship between brood size and fledging success

The mean±SD number of filial fledglings per brood was 1.1±1.16 in low-predation areas ($n=138$ broods) and 0.6±0.95 in high-predation areas ($n=119$) (GLME, $F_{1,235}=12.097$, $p=0.040$). The number of all fledglings produced per brood showed a positive relationship with brood

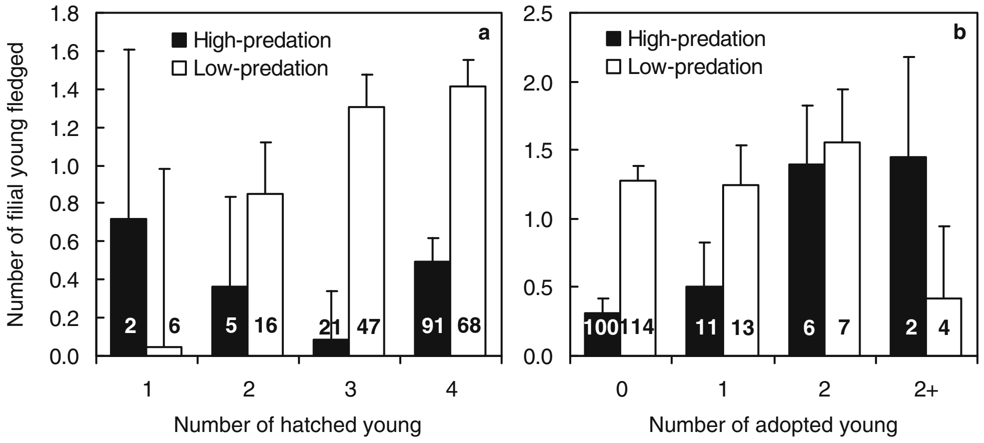

Fig. 1 Mean+SE number of filial fledglings by **a** the number of young hatched and by **b** the number of naturally adopted young in broods of pied avocets nesting in high-predation areas (drained fishpond/reconstructed wetland) and low-predation areas (alkaline lakes) in south-central Hungary between 1998 and 2000. Means adjusted for hatching date are shown; sample sizes (number of broods) are at the base of *bars*

size (GLME, $B=0.32\pm$SE 0.058, $F_{1,235}=31.550$, $p<0.0001$). Brood size also significantly and positively influenced the number of filial young fledged per brood (GLME, $B=0.18\pm$ SE 0.050, $F_{1,235}=13.002$, $p=0.0004$).

Importance of brood size components under different predation

In low-predation areas, the number of filial young fledged increased with the number of young hatched (Fig. 1a, Table 2). However, the number of filial fledglings was not related to either the number of naturally adopted chicks or the number of experimentally added chicks (Table 2). In contrast, the number of filial fledglings decreased by both the experimental removal of chicks and the natural loss of chicks in the colony (Table 2). Finally, the number of filial fledglings decreased as season progressed in low-predation areas (Table 2).

In high-predation areas, the number of filial fledglings increased only with the number of naturally adopted chicks and was not related to the number of young hatched or to hatching date (Fig. 1b, Table 2). Chick loss in the colony by natural reasons decreased the number of filial fledglings significantly, whereas the experimental removal of chicks did not affect fledging success (Table 2). The experimental addition of chicks decreased the number of filial fledglings in high-predation areas from 0.5±(SE) 0.12 chicks in

Table 2 Influence of brood size components, hatching date and brood-rearing area on the number of filial young fledged per brood in pied avocets nesting in low-predation areas and in high-predation areas in south-central Hungary between 1998 and 2000

Effect	Coefficient	SE	*df*	*t*	*p* value
Low-predation areas ($n=138$ broods)					
(Intercept)	1.97	0.755	116	2.605	0.0104
Number of hatchlings	0.43	0.104	116	4.125	0.0001
Number of experimentally added chicks	−0.11	0.360	116	−0.304	0.7616
Number of experimentally removed chicks	−1.02	0.360	116	−2.831	0.0055
Number of naturally adopted chicks	−0.18	0.099	116	−1.808	0.0732
Number of naturally lost chicks	−0.44	0.140	116	−3.141	0.0021
Hatching date[a]	−0.03	0.010	116	−2.928	0.0041
High-predation areas ($n=119$ broods)					
(Intercept)	0.61	0.722	107	0.843	0.4009
Number of hatchlings	0.21	0.128	107	1.676	0.0966
Number of experimentally added chicks	−0.46	0.184	107	−2.504	0.0138
Number of experimentally removed chicks	−0.30	0.194	107	−1.572	0.1190
Number of naturally adopted chicks	0.46	0.119	107	3.898	0.0002
Number of naturally lost chicks	−0.29	0.125	107	−2.309	0.0229
Hatching date	−0.01	0.010	107	−1.345	0.1815
Brood-rearing area	−0.08	0.174	107	−0.439	0.6618

Parameter estimates were obtained by generalized, linear mixed-effects models with natal colony nested within natal lake as a random block effect. Many pairs in high-predation areas left the natal lake with their broods to move towards low-predation areas and suffered the highest predation (Lengyel 2006), therefore, brood-rearing area was included as a binary predictory variable (remaining or leaving high-predation area) for broods in high-predation areas. The random effect was not influential in either model (intercept SD < residual SD).

[a] Number of days since March 15 until hatching of the first chick

unmanipulated broods (n=81) to 0.1±1.38 in broods containing experimentally added chicks (n=38; Table 2). This was mostly because one filial chick was removed as part of the experiment in half of the broods with experimentally added chicks (modified broods, n=19). In addition, modified broods also suffered disproportionate chick loss in the colony. Ten (or 53%) of the 19 modified broods in high-predation areas lost chicks to natural causes in the colony, whereas this proportion was between 8 and 33% in other groups (Table 1). The proportion of loss was similar for filial chicks (6 or 12% fledged of 47) and experimentally added chicks (4 or 21% of 19; Fisher exact test, p=0.456). The low number of filial fledglings in broods with experimentally added chicks could not be attributed to either chick body size or weather parameters during week 1 post-hatch (GLME refitted with the above variables as covariates; chick body size $F_{1,62}$=1.123, p= 0.293; average daily temperature during week 1 post-hatch $F_{1,62}$=0.126, p=0.724; number of storms during week 1 post-hatch $F_{1,62}$=0.410, p=0.524).

The relationship between brood size and prey abundance

In low-predation areas, there was a positive relationship between the size of a pair's brood and prey abundance on their first stationary territory (Fig. 2). However, a non-significant interaction (p=0.081) suggested important differences among years. The relationship was strongest in 1998 (driest year), when alkaline lakes almost dried out, prey abundance was low and thus, brood-rearing areas were limited. In contrast, the relationship was weak in the extremely wet 2000 (Fig. 2), when high precipitation resulted in large areas with shallow water and high prey abundance suitable for brood-rearing. Hatching date did not influence these patterns (GLME, year $F_{2,10}$=82.959, p<0.0001; brood size $F_{1,33}$= 9.055, p=0.005; year × brood size interaction $F_{2,33}$=2.736, p=0.080; hatching date $F_{1,33}$=1.553, p=0.222).

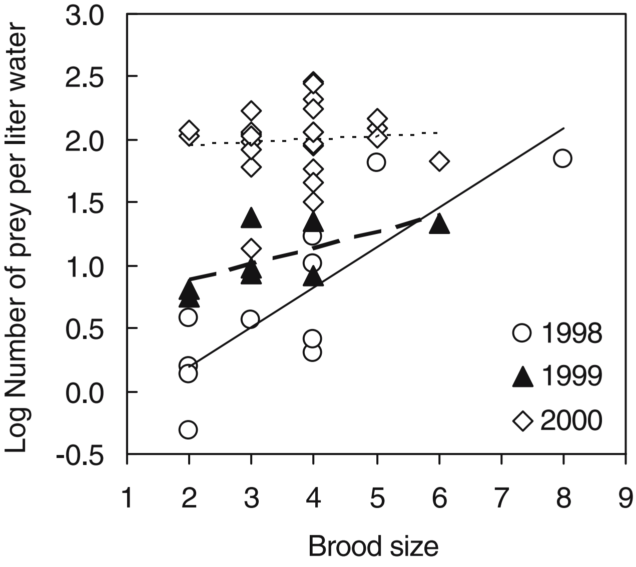

Fig. 2 Prey abundance on the territory as a function of brood size at the departure of pied avocet broods from the colony in low-predation areas. Generalized linear mixed-effects model with brood size and year as fixed effects and natal colony nested within natal lake as random factor, n=52 broods, year $F_{2,10}$=60.827, p<0.0001; brood size $F_{1,34}$=8.570, p=0.006; interaction $F_{2,34}$=2.703, p=0.081

Do pairs gain by adoption?

Pairs that naturally adopted chicks fledged on average twice as many filial young in their broods (1.6±0.92, n=21 pairs) as did non-adopting, non-donor pairs (0.8±1.11, n=122) or donor pairs (only filial young remaining in donor broods are included, 0.8±0.97, n=17; GLME, adoption status $F_{2,138}$= 3.304, p=0.040). The effect of adoption status remained significant when brood size and hatching date were controlled for (adoption status $F_{2,136}$=3.755, p=0.026; brood size $F_{1,136}$= 11.113, p=0.001; hatching date $F_{1,136}$=5.460, p=0.021).

These differences, however, depended on habitat. Adopting pairs fledged significantly more young than non-adopting, non-donor pairs in high-predation areas, whereas a similar pattern in the number of fledglings (adopter > donor > non-adopter/non-donor) was not significant in low-predation areas (Fig. 3). Donors and non-adopters/non-donors produced similar numbers of filial young in their own broods in both areas. However, when donors' chicks raised in adopting broods were included, the number of fledglings by donors was slightly but not significantly higher than that by non-adopters/non-donors (1.1±0.97 for the two habitats combined; Fig. 3). Donors especially gained by adoption in high-predation areas where the number of fledglings produced by them doubled by adoption (Fig. 3).

Do chicks gain survival benefits by adoption?

Chick status (naturally adopted, resident in naturally adopting broods, resident in donor broods or resident in intact broods) did not influence whether chicks fledged or not (logistic regression using hierarchical GLME with chick status as within-subject factor and natal colony, hatching date and brood size as between-subject factors with brood as random factor; chick status $F_{3,347}$=2.009, p=0.112). Fledging success was 36% for naturally adopted chicks (n=28), 39% for resident chicks in donor broods (n=33 chicks), 52% for residents in naturally adopting broods (n=65 chicks) and 27% for chicks in broods not involved in adoption (n=388).

Is adoption related to parental quality?

To test whether adopters are higher quality individuals than are non-adopters or donors, I compared egg-laying date,

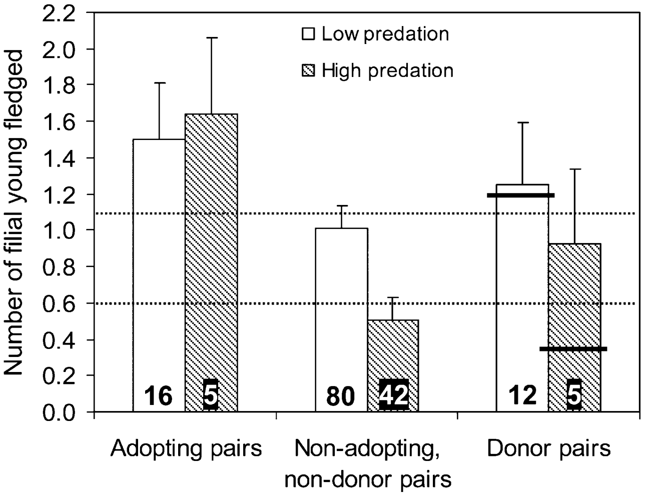

Fig. 3 Mean+SE number of filial young fledged by pairs adopting chicks, pairs not adopting and not losing chicks to adoption and pairs losing chicks to adoption (donors) in low-predation and high-predation areas. Data are from non-experimental broods only (n=160), and means are statistically adjusted to significant covariates (GLME models with adoption status as main effect, brood size and hatching date as covariates and colony nested within natal lake as random factor; low-predation areas: adoption status $F_{2,87}$=0.233, p=0.792; brood size $F_{1,87}$=5.404, p=0.022; hatching date $F_{1,87}$=6.377, p=0.013; adoption status × brood size interaction $F_{2,87}$=1.981, p=0.144; high-predation areas: adoption status $F_{2,40}$=12.018, p<0.0001; brood size $F_{1,40}$=7.462, p=0.009; hatching date $F_{1,40}$=0.883, p=0.353; adoption status × brood size interaction $F_{2,40}$=0.297, p=0.744). Sample sizes (number of broods) are at the base of *bars*; *dotted lines* indicate the mean number of fledglings in low-predation areas (1.1) and in high-predation areas (0.6). *Thick lines* in *donors'bars* indicate the mean number of fledglings produced by donors, excluding their chicks raised in adopting broods

egg and clutch size, number of young hatched and chick body size among adopters, donors and non-adopters/non-donors. Pairs that adopted chicks laid their first eggs slightly earlier (Julian date of egg-laying: 54±9.2 days, n=21 pairs) than donors (56±6.2 days, n=17) or non-adopters/non-donors (59±12.9 days, n=122; GLME, $F_{2,138}$=6.102, p=0.003). However, this pattern could also be explained by a higher density of simultaneously hatching broods early in the season, and thus, more opportunities to adopt for early nesting vs later nesting pairs. The probability of adoption, i.e. whether a pair adopted chicks or not, increased with the number of simultaneously (±1 day) hatching broods within the colony and decreased with season (logistic regression using GLME; number of same-aged broods: B=0.11±SE 0.053, $F_{1,234}$=4.716, p=0.031; hatching date: B=−0.05±SE 0.020, $F_{1,234}$=7.730, p=0.006; number of broods × hatching date interaction $F_{1,233}$=0.986, p=0.325). Finally, there was no difference among adopters, non-adopters/non-donors and donors in any other studied measures related to parental quality (clutch size, egg size, number of young hatched or chick body size; results not shown).

Discussion

This study is the first to reveal benefits of larger-than-normal broods in shorebirds. The benefits of large broods depended on habitat because different brood size components influenced the number of fledglings in low-predation and high-predation areas. When predation was low, only the number of young hatched had a positive effect on the number of young fledged, and the positive correlation between brood size and prey abundance on the territory showed that larger broods may occupy better territories than smaller broods. This result supports the brood-dominance hypothesis, which predicts that larger broods access better resources than smaller broods due to their increased social dominance (Black and Owen 1989a; Kehoe 1989; Loonen et al. 1999; Öst and Kilpi 2000; Williams 1994). For example, adults with larger broods may be more motivated to initiate social interactions, whereas those with smaller broods may be less motivated to engage in such interactions (Black and Owen 1989a). Avocet adults defend their territories against both adults and chicks (Cramp and Simmons 1983; Lengyel et al. 1998), thus, it appears plausible that brood size plays a role in territorial interactions. These benefits, however, may be limited to conditions when competition for resources is high (Loonen et al. 1999; Mulder et al. 1995; Williams 1994). The annual differences in the relationship between brood size and prey abundance correspond to this explanation. The relationship was strongest in the driest year (1998), when potential brood-rearing areas were limited and prey abundance was low, and it was weak in 2000, when extensive shallow water surfaces were available for brood-rearing and average prey abundance was at least an order of magnitude higher than in the dry year (Fig. 2).

When predation was high, the number of filial fledglings increased with the number of naturally adopted chicks (Fig. 1b), and naturally adopting pairs fledged more young than did non-adopting, non-donor pairs. These results, and the absence of such relationships in low-predation areas, suggest that brood size increase was related to higher survival of filial chicks under high predation. The results thus support the dilution-of-predation hypothesis, which predicts that the presence of non-filial chicks in the brood can decrease the chance that a filial young is depredated (Pierotti 1991). Such dilution of predation may explain brood amalgamation in the common eider and in the white-winged scoter because ducklings in larger broods have a survival advantage over ducklings in smaller broods (Gorman and Milne 1972; Kehoe 1989; Munro and Bedard 1977). The survival advantage may arise by better detection of predators or by better defense against predators by more young present or by more motivated adults. Large groups of chicks may also be more efficient at confusing predators or disrupting their attacks (Hamilton 1971). Such anti-predator benefits of large broods also have been presumed in shorebirds, e.g. in bristle-thighed curlews (*Numenius tahitiensis* Gmelin; Lanctot et al. 1995).

On the chicks' side, however, gaining adoption into another brood did not lead to higher chances of fledging. Chick status did not influence whether chicks fledged or not, and the proportion of fledging was similar for naturally adopted chicks (36%) and their siblings (residents in donor broods, 39%). These results suggest that it is unlikely that adoption in avocets is driven by the interests of the chicks of the donor parents. Rather, my results support the hypothesis that adoption can be explained by a non-adaptive drive by young chicks to join groups of other chicks, and that the benefits of larger broods are reaped by the adopting parents. The existence of the drive by chicks to join groups of chicks is supported by three findings. First, adoptions were more likely to occur when more broods were hatching simultaneously in the colony than when fewer broods were hatching at the same time. Second, broods enlarged in the experiment apparently became more attractive to chicks seeking adoption because 31% of the enlarged broods adopted chicks compared to 0–13% in the other experimental groups (Table 1). Finally, chick loss between the manipulation and brood departure from the colony was more frequent in experimental broods where brood size was reduced or unchanged (5 of 15 reduced broods and 10 of 19 modified broods lost chicks) compared to experimental broods where brood size was increased (2 or 8% of 26 enlarged broods lost chicks; Table 1).

Corresponding to the results on the effect of brood size components on fledging success (Table 2), pairs that adopted chicks fledged more of their own filial young than pairs not adopting chicks or losing chicks to adoption in high-predation areas but not in low-predation areas. Although the difference was in a similar direction in low-predation areas (Fig. 3), the effects of brood size and hatching date were both significant (the latter only in such areas) and may have masked the effect of adoption status. These results suggest that whether a pair adopted or not was of secondary importance compared to when they started egg-laying and how many eggs they hatched in low-predation areas.

Although donor pairs did not fledge more young in their broods than non-adopters/non-donors, the total number of fledglings produced by donors was similar to that produced by adopters under both low and high predation. This result suggests that donor parents do not suffer fitness costs by losing chicks to adoption. Alternatively, it is also possible that pairs that lose chicks to adoption exploit the parental care of adopting pairs, which obtain direct reproductive benefits in other ways, e.g. through an increased brood size. Such a strategy may exist, for example, if both adopters and donors are relatively high-quality individuals, and no significant costs occur on either side. Although data on the start of egg-laying correspond to this explanation because both adopters and donors laid eggs a few days earlier than non-adopters/non-donors, such a pattern also could be explained simply by the higher availability of source broods earlier than later in the season. Furthermore, there was no difference among adopters, non-adopters/non-donors and donors in any other studied measures related to parental quality. Considering also that direct measures of adult quality (e.g. age and body size) were not available for testing, the results of this study do not corroborate but neither falsify the hypothesis that brood size benefits may be related to differences in parental ability among adults.

Parental quality also may interact with brood size benefits through nesting site selection if high-quality pairs (e.g. experienced parents) settle in safer sites. However, such a scenario is unlikely in this study. Nesting started 10–12 days earlier in high-predation areas (semi-natural sites) than in low-predation ones (natural habitats) despite the apparently similar availability of nesting sites in both areas in each year (Lengyel 2006). Earlier initiation of colonies may indicate that avocets prefer semi-natural sites for nesting and that earlier-breeding birds that are probably of higher quality than later nesting birds settle in semi-natural sites. However, pairs nesting in high-predation and in low-predation areas did not differ in clutch size, egg size, number of chicks hatched or body size of their chicks. The lack of such differences makes it unlikely that nest site selection is related to parental quality in the studied group of avocets.

There was an important difference in whether brood size changed by natural adoption or by experimental enlargement because natural adoptions led to more filial fledglings, whereas experimental enlargement resulted in no increase (low-predation areas) or a drop (high-predation areas) in the number of filial fledglings. One possible explanation is that naturally adopted chicks, which were somehow 'motivated' to seek adoption into another brood, may be better integrated in the foster brood through imprinting processes than are randomly added chicks, which lacked motivation and were 'forced' to gain adoption. Experimentally added chicks, which did not go through the process of natural adoption, for example, may be located farther from the vigilant adult or may not follow the leading adult as closely as do filial or naturally adopted chicks. Compared to naturally adopting broods, therefore, the integrity of experimental broods may have been lower. Brood integrity was probably important in high-predation areas where territorial aggression among adults and disturbance by predators often disrupted broods physically. The risk of predation may be higher for less integrated and more dispersed broods in shorebirds and geese (Safriel 1975; Lessells 1987; Mulder et al. 1995; Székely and Cuthill 2000), therefore, it is possible that the lower chick survival in manipulated broods, especially in modified broods, is related to the lower integrity of such broods. Experimental enlargement also has resulted in lower fledging success in both of the other two brood manipulations in shorebirds (Safriel 1975; Székely and Cuthill 2000). In semi-palmated sandpipers (*Calidris pusilla* L.), broods enlarged by one chick were more conspicuous and more prone to predators than were non-manipulated four-chick control broods (Safriel 1975). In Kentish plovers (*Charadius alexandrinus* L.), brood survival decreased with manipulated brood size, especially in the early part of the breeding season (Székely and Cuthill 2000). However, larger, non-experimental broods did not suffer higher predation in this study. Furthermore, manipulations in precocial birds other than shorebirds also have not found increased chick mortality in enlarged broods (Lessells 1986; Milonoff and Paananen 1993; Rohwer 1985; Sandercock 1994; Williams et al. 1994). These results suggest that random manipulations may not be efficient in detecting brood size-related benefits in shorebirds because the higher initial mortality of chicks in experimental broods prevents the pairs from realizing the benefits that manifest later in brood-rearing.

This study shows an important difference in the role of chick adoption in the life history and parental investment between precocial birds that do not feed their young (e.g. rheas *Rheidae*, geese, swans and ducks *Anseriformes*, waders *Charadrii*, grouses and turkeys *Galliformes*) and altricial or semi-precocial birds that feed their young (e.g. gulls and terns *Laridae*, pelicans *Pelecaniformes*, doves *Columbiformes*, swifts *Apodiformes*, owls *Strigiformes* and passerines *Passeriformes*). Chick adoption in semi-precocial or altricial birds is driven mainly by the evolutionary interest of chicks receiving inadequate care in the natal brood (Pierotti and Murphy 1987), and adopting adults usually pay the costs of provisioning larger broods by poorer body condition, lower subsequent survival or fecundity (summarized in Table 1 in Golet et al. 1998). In precocial birds, however, brood-rearing costs are minimal, or brood size is associated with reproductive benefits by increased brood dominance, as in some geese, or lower chick mortality, as in some ducks, which may similarly benefit adults and young. The pied avocet is the first species in which both kinds of benefits are detected. However, the benefits appear applicable in several other taxa that have a natural history similar to that of avocets and may be related why natural adoption or brood amalgamation is common in shorebirds (Cooper and Miller 1992; Hale 1980; Lanctot et al. 1995) and in other precocial birds (e.g. Codenotti and Alvarez 1998; Mills and Rumble 1991; Skutch 1976; Kraaijeveld 2005).

In conclusion, large brood size provided reproductive benefits under both low and high predation in avocets. Such benefits may increase annual and ultimately, lifetime reproductive success. However, when clutch size is limited, as in shorebirds, increasing the size of the brood is only possible by deploying some alternative reproductive tactic. In avocets, chick adoption appears to fulfill this role and to enable certain parents to increase their reproductive success. Further study is necessary to evaluate the roles that parental quality and genetic relatedness between adopter and adoptee play in the evolution of adopting behaviour in shorebirds.

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