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Parental sex roles of Malaysian plovers during territory acquisition, incubation and chick-rearing

M. Yasué · P. Dearden

Abstract Shorebirds show high variability in parental care strategies among species, populations, and environments. Research on shorebird parental sex roles can help to understand the selective pressures that shape avian breeding strategies. Although several studies have examined parental care strategies in holarctic shorebirds, very little research has been conducted in the tropics. Here we examined parental sex roles during territorial defence, incubation, and chick-rearing in Malaysian plovers *Charadrius peronii* in the Gulf of Thailand. The costs and gains of particular parental behaviour may vary between the sexes and can be affected differently by environmental factors and chick age. Thus we also examined how temperature, prey availability, chick or embryo age, and time of day affected parental sex roles. Males spent more time defending territories and were further away from chicks whereas females spent more time incubating eggs. Both adults contributed to chick defence during disturbances throughout the entire chick-rearing period. Total nest attendance (sum of both sexes) was affected by the modelled temperature of an unincubated egg. Prey availability, embryo age, and time of day had no effect on total nest attendance. Males adjusted incubation effort in response to temperature only at high temperatures (>36°C) whereas females adjusted nest attendance at high and low temperatures. Chick age had no effect on the proportion of time adults spent defending territories or responding to distur-bance. Pairs were more likely to fledge chicks if both the male and female spent more time defending territories. For Malaysian plovers, high cooperation between the sexes during parental care may help to achieve high quality breeding territories, maintain body conditions during hot days, protect offspring from predators and attacking conspecifics, and contribute to high lifetime reproductive success.

Keywords Incubation · Parental care · Plover · Shorebird

Introduction

In shorebirds, parental care can vary among and within species, from equally shared biparental care to unipa-rental care by either the male or female (sub-order *Charadrii*). Because of this diversity, shorebirds have been used as model taxa to examine how selective pressures relating to the physical or social environment shape parental sex roles (Reynolds and Székely 1997; Székely et al. 2006).

Animals adjust parental investment on the basis of a trade-off between current and future reproductive success (Clutton-Brock 1991). Sexual differences in parental care may occur because the fitness costs and benefits of territory defence, incubation, or brood-care can differ between sexes (Brunton 1988; Clutton-Brock 1991). One of the key features causing sex-based dif-ferences in behaviour of birds is that females must acquire energy and calcium reserves to lay eggs (Breitwisch 1989; Székely and Lessells 1993). Conse-quently females may reduce parental effort during periods when they are energetically constrained and

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could jeopardize future breeding success such as during or immediately after egg-laying, or in the last week of chick-rearing (Székely and Williams 1995). Energy factors may be particularly important in affecting female parental care for species that nest more than once during a breeding season, have short inter-clutch intervals, or undergo a costly migration immediately after breeding (Graul 1976; Sandercock et al. 1999).

Although males do not incur egg-laying costs, they could expend significant resources defending territories (Burger 1981). Territory defence can improve breeding success by protecting resources, reducing infanticide, and attracting potential mates (Dubois et al. 1998). In addition to these benefits, which are shared between the mates, males may gain more from defending territories than females because by preventing other males from entering territories males may reduce the risk of cuckoldry (Nol 1985; Zharikov and Nol 2000). Consequently, for non-polyandrous shorebirds, males may spend more time defending territories than females, particularly before egg-laying when females are fertile (Brunton 1988).

The relative costs and benefits of egg formation, territory defence, and parental care depend on breeding stage and a complex range of interacting environmental, ecological, social or genetic factors. For example, female shorebirds that do not migrate and breed in highly productive environments with high chick depredation rates may contribute more to parental care because they can more easily obtain the energy reserves necessary to recoup the costs of egg production and because they can significantly enhance chick survival by contributing to chick defence (Amat et al. 2000; Wallander and Andersson 2003).

Although many studies have demonstrated how these types of environmental, ecological, or social conditions affect shorebird breeding strategies and parental care (Blomqvist et al. 2001), virtually all of the research has been conducted in temperate or arctic environments (Thomas et al. 2003; Moreno 2004). Very little is known about the ecology of any of the 32 plover species that breed mainly in the tropics. The longer breeding seasons, stable weather conditions, high and diverse predation pressures, and shorter migration routes of most tropical species (Martin 1996; Moreno 2004; Weatherhead and Blouin-Demers 2004) are likely to affect parental behaviour. More studies on parental care in tropical species are needed to describe parental behaviour and also identify factors that shape avian breeding ecology under a wider range of environmental or ecological conditions.

Here we describe the parental sex roles of Malaysian plovers *Charadrius peronii*, a near-threatened,

beach-nesting shorebird breeding on beaches and wetlands in the Gulf of Thailand. We monitored the plovers from November to July and compared territorial effort, nest attendance, chick defence and vigilance, and feeding rates between the sexes. Apart from an anecdotal note (Gregory-Smith 1998) and general distribution information (Collar et al. 1999; Smythies and Davison 1999; Robson 2002), there are few detailed, published studies on this species (Yasué and Dearden 2006a, b, c). The Malaysian plover is an ideal species to explore some of the possible differences between parental roles in temperate and tropical areas, because there are several well-studied temperate populations of closely related species such as the common ringed plover (*Charadrius hiaticula*), and temperate populations of Kentish plovers (*Charadrius alexandrinus*) (Purdue 1976; Fraga and Amat 1996; Wallander 2003).

Within a population, many factors can alter the parental investment trade-offs (Székely and Williams 1995; Székely and Cuthill 1999) and lead to changes in the sex-roles. In this study we also examined whether temperature, prey availability, and chick age had different effects on parental care behaviour of males and females. This part of our study enables finer resolution of the partitioning of parental care and helps to evaluate how environmental constraints shape breeding strategies.

Because ambient temperatures rise above optimum incubation temperatures (35–37°C) (Webb 1987), one or both adults will increase nest attendance because exposed clutches become more vulnerable to heat-induced mortality (Dunning and Bowers 1990; Weston and Elgar 2005b; Yasué and Dearden 2006b). Heat stress may also result in greater costs to the body condition of incubating parent (Carey 1980; Conway and Martin 2000). Prey density could also affect nest attendance, because plovers in territories with low prey availability may spend less time incubating nests and more time feeding (Erckmann 1983).

The change in male or female nest attendance because of these environmental conditions depends partly on mate fidelity for future breeding attempts and paternal certainty. For species with high mate fidelity within or between years and generally low rates of extra-pair copulations (EPCs) the cost of nest failure is more similar between mates (Reynolds 1996) and individual lifetime reproductive success is affected more by the condition of the mate (Wittenberger and Tilson 1980). Consequently pairs may cooperate and adjust behaviour in response to varying environmental factors to successfully defend high-quality territories, maximize the survival of the current brood, and retain

body condition of both sexes for future breeding attempts with the same mate in the same or future years (Pierce and Lifjeld 1998; Cuervo 2003). In these types of breeding system, if females have difficulties recovering body condition after laying eggs, males may be more likely to increase nest attendance during hot weather and also contribute more to nest attendance in areas with low prey availability compared with females.

Alternatively, for species with lower mate fidelity or if one of the mates is able to re-nest with a different mate in a season, there could be conflicts between the sexes on the value of the current brood and the appropriate amount of parental investment (Slagsvold et al. 1995; Ackerman and Eadie 2003). In these types of breeding system the cost of current nest failure could be greater for females because of higher parental certainty (Westneat and Sargent 1996). For this reason, females may be more likely to increase nest attendance during periods of heat stress or in environments with low prey availability.

Methods

Study area

All data were collected on beaches between Bornok village (99°53′ 12°00′) in Prachuap Khiri Khan and Laem Phak Bia village (100°05′ 13°03′) in Petchburi province in the Gulf of Thailand between 20 November 2003 and 25 July 2004 and between 10 January and 28 July 2005. In this region, there is a hot, humid and sunny summer from April to May (diurnal 28–42°C) and a cloudier rainy season from June to July (diurnal 26–38°C).

Nest monitoring

Malaysian plovers defend 100–300 m long multi-purpose rectangular territories that include an intertidal mudflat foraging area, a sandy beach for nesting, and a shrubby vegetated area behind the beach that provides cover for chicks during disturbances (Yasué and Dearden 2006c). Beginning in April, they lay two to three cryptic eggs in shallow scrapes. The eggs in a clutch hatch over 1–3 days after a 30-day incubation period. The chicks are precocial, never fed by parents, and fledge after 27–35 days (Yasué and Dearden 2006a, b, c).

During the breeding season we found nests by searching in areas where pairs were frequently observed or by watching birds return to nests. We used a Garmin 60 GPS unit to record nest locations. Eggs were floated regularly to detect embryo mortality, estimate lay and hatch date, on the basis of a 30-day incubation period, (Yasué and Dearden 2006a, c). We checked the nests every 3–5 days to determine nest survival or cause of failure. All eggs were weighed using a 10 g spring balance Pesola scale. Most adults were caught and banded either during the preceding winter (only in 2003/2004), summer, or on nests using noose mats or funnel traps (Mehl et al. 2003) (number of banded adults/chicks 2004 and 2005: 118/88, 75/103). We captured and individually colour-banded chicks within two weeks of hatch and returned to the nesting territories weekly to assess chick survival up to 30 days. After catching birds we did not conduct any behavioural observations on those individuals on the same day.

In total, 86 and 126 nesting attempts of 54 and 79 pairs were monitored in 2004 and 2005. Family groups could be identified because at least one of the chicks or adults was individually colour-banded. It was possible to assess fledgling success accurately because broods did not move more than 300 m from nest sites. There were 80 banded breeding birds at the end of the field season in 2004 and 42 returned to breed within the study area in 2005.

Sex ratios in winter flocks

In the non-breeding season, Malaysian plovers roost in tight flocks on wide beach sections at high tide. Although these winter flocks are likely to have several purposes, for example reduced predation risk (Cresswell 1994) or mate selection, birds in these flocks also began defining territories and frequently stop roosting to display or fight amongst each other. Thus sex biases in these flocks could indicate differential effort in breeding territory acquisition or unequal sex ratios (Székely et al. 2006). We counted the total number of males and females in these winter flocks on the basis of obvious plumage differences (Robson 2002) to determine whether there was any difference between the sexes in pre-breeding site occupancy effort. Males have black crown, eye, and chest bands, and more extensive cinnamon on their head than females (Robson 2002). One hundred and thirty nine counts for flocks with more than five individuals were conducted in five different locations and days between November 2003 and March 2004 and from January to March 2005. If the same location was sampled more than once during a day, mean values were calculated. These five locations were at least 6 km apart and based on observations of banded individuals, adults plovers did not move among these locations. Thus we could assume these sampling

sites were independent of each other. We calculated mean values of the number of males and females per location.

Incubation observations

We watched incubating plovers using a 15–45 × spotting scope and 10 × 50 binoculars for a total of 163 h from either a hide or a seated position on the mudflat located more than 150 m from the plovers. Nest observations lasted 1–2 h (mean length = 75.7 ± 2.3 min; all measures of dispersion here and throughout the text and figures are standard error) and were conducted on 113 different nests (at least 82 known colour-banded pairs [up to 95]) between April and July in 2004 and 2005. The duration of the nest observations depended partly on the incubation bout length. We ensured that in all observations in which adults visited the nest at least once we were able to record at least one complete incubation bout that was not disturbed by the observer. The length of incubation bouts for Malaysian plovers is shorter than for temperate or Arctic species, probably because heat stress forced the adults off the nests.

During nest observations we recorded the start and end times of incubation bouts. *Total nest attendance* was the percent of time during a nest observation in which either the male or female incubated the eggs. Male and female attendance refers to the proportion of the nest observation in which each sex attended nests.

Egg temperature model

We modelled the egg temperature of an unshaded clutch from measurements of shaded air temperature, cloud cover, and time of day that we made incubation observations. We developed the exposed egg temperature model by measuring the temperature inside similar sized and pigmented quail (*Coturnix coturnix*) eggs in recently abandoned Malaysian plover nest cups on 42 different occasions (Appendix). The methods used to develop the model have been described in detail elsewhere (Yasué and Dearden 2006b).

Prey availability

Small *Scopimera* (bubbler) crabs are a major prey of Malaysian plovers (Yasué and Dearden 2006c). We measured prey availability along 200-m (parallel to the beach) intertidal mudflat sections in front of each Malaysian plover nest. At each mudflat sampling section we measured the width of the mudflat

(perpendicular to the beach) where crab burrows were present. We paced the mudflat and visually estimated the proportion of the area with high (>100 m^{-1}), medium (20–100 m^{-1}) or low crab densities (<20 m^{-1}). These proportions were used to calculate weighted average crab densities for the sections. For each of the three density categories we counted all 2–10 mm diameter burrows in two 0.46 m^2 randomly placed quadrats. We then multiplied the width of the mudflat with weighted average burrow densities to calculate an estimate of crab abundance for the sampling section. All crab prey sampling was conducted between 08:00 and 13:00, 0.7–1.0 m above lowest low water (based on published tide table values) from 15 to 25 July of 2004 and 2005. Although direct counts of *Scopimera* densities would have yielded more accurate estimates of prey availability than burrow counts, our method was necessary because of the large number of sites that had to be sampled over a short period (Yasué and Dearden 2006c). Burrows were, moreover, a good indicator of crab availability because crabs created burrows at every low tide period to feed at the surface (Takahashi et al. 2001).

Although our prey sampling period was late in the breeding season, the adults (and chicks if breeding attempts were successful) still remained in the territory when we were sampling. Because pairs nested several times in the same territory, it is likely that pairs remained together defending the territory even after chicks fledged or a breeding attempt failed, because of the possibility of nesting again within the season.

Sex roles during chick-rearing

We conducted 109 h of brood watches at 57 different nesting attempts from a hide or a seated position at least 200 m away. Chick-rearing observations lasted 45 min to 1 h (mean length = 50.2 ± 1.3 min).

We conducted scan samples and recorded the behaviour of the adults and chicks every five minutes as well as any types of anthropogenic or natural disturbance (Martin and Bateson 1986).

Behaviour was categorized in the following manner:

Disturbed = Neck out-stretched vigilant posture, flushing to the mudflat from nest, "rat-running", calling to distract predators, false brooding, or crouching (Gochfeld 1984).
Territorial = Fluffed out feathers and displaying to, chasing, or fighting with conspecifics.
Roosting = Body trunk on the ground, or eyes shut and feathers fluffed, preening feathers or bathing.
Feeding = Pursuing prey.

Incubating = Incubating eggs (occurs when chicks hatch asynchronously or successive clutches are laid before primary clutches fledge and one adult incubates clutches while the other cares for the chicks). *Brooding* = Shading or brooding chicks.

We also estimated the distances between chicks and parents by counting body lengths or by comparison with known distances. If there was more than one chick in the brood we estimated the distance from the adult to the nearest chick.

Malaysian plovers may have biparental care throughout the breeding season because both parents are required to defend chicks from predators and to fledge chicks. In 71 brood observations people or potential predators disturbed broods at least once. We examined how chick age affected the frequency of disturbance responses that were male-only, female-only, or biparental.

Focal observations

In addition to nest or brood observations we conducted 5–25-min focal observations using hand-tallies and timers to measure adult activity budgets (Martin and Bateson 1986). These focal observations were conducted between November and July and enabled us to detect any behavioural differences between males and females before and during the breeding season. During all observations we recorded the breeding status of the bird (pre-breeding, inactive, incubating, or chick-rearing, where *pre-breeding* pairs were pairs that had not yet laid clutches that year, usually November–March, and *inactive* birds were birds that had recently failed or fledged a chick, and not yet re-nested).

Finer behavioural categories were used during focal observations to detect rare or inconspicuous behaviour that may not be observed during brood observations. The roosting category used in brood observations was divided into resting, preening, and bathing. We also included a category for courtship behaviour (nest building, copulating, or displaying to mates). For feeding, we counted the number of attempted feeding attempts rather than the total amount of time birds appeared to be feeding. This approach was necessary to reduce ambiguity and facilitate comparisons among birds at different stages of breeding, because feeding birds were often also engaged in other activities, for example defending territories or watching chicks.

During focal observations ''disturbance'' behaviour did not include neck-outstretched vigilance behaviour and only included times when birds were using calls and displays to distract predators, running or flying away

from disturbances, or crouching to hide from avian predators. This distinction was necessary because when adults were not rearing chicks it was often difficult to discern between vigilance from predators and standing and looking for prey or intruding conspecifics. When adults were with chicks it was easier to discriminate between vigilance behaviour and other non-disturbance-related behaviour because adults were usually facing toward chicks and also frequently on the beach (rather than the mudflat feeding area). We also included one other category, ''standing'', to describe birds which were not overtly engaged in any of the other activities. In this position, birds may be passively looking for predators, prey, or conspecifics or resting (but not sitting, preening, or bathing). We did not conduct focal observations on plovers that were incubating nests.

We were able to ensure that an individual was not sampled more than once a day because the birds were highly territorial and 65% (2004) and 70% (2005) of the birds were individually colour-banded.

Statistical analyses

All data analyses were two-tailed and conducted using SPSS version 11 (SPSS 2001).

We used a paired *t*-test to evaluate whether there was any difference between the number of males and females in flocks at the five roosting areas before the breeding season.

Multiple incubation observations were taken from the same pair at the same nest, at different nests, or between years. The total number of samples per individual ranged from 1 to 10 observations. We could not conclusively determine whether we re-sampled the same individuals between years, because not all individuals were colour-banded. For incubation observations, however, we randomly sampled one observation for each known pair in which we conducted multiple watches. Only one sample was taken for each pair between the 2 years. This approach was used instead of taking mean values of male and female attendance, because temperature has a strong effect on incubation behaviour (Yasué and Dearden 2006b) and mean values would obscure this effect. We used a Wilcoxon's signed rank test of related samples to determine whether males and females had significantly different attendance during 82 nest observations.

We used binary logistic regression to test whether modelled egg temperature, prey availability (crab burrow relative density), embryo age (measured as weeks into the incubation period, 1–4), and time of day affected total, male, and female nest attendance. Time of day was included in the model to account for

non-temperature-related factors, for example predation or prey availability, that could vary during the day. The incubation requirements of clutches may vary in quadratic or linear functions, because birds must warm eggs at low temperatures and shade eggs at very high temperatures. Consequently we included both linear and quadratic terms for modelled egg temperature.

To conduct binary logistic regression, we categorised the three dependent variables into two equal-sized classes [total attendance > 80% or ≤ 80%, male contribution (> 17% or ≤ 17%) and female contributions (> 49% or ≤ 49%)]. Binary logistic regression was used because data were not normally distributed and could not be normalized using standard data transformations, because of the large numbers of zero values. To ensure the robustness of our models we re-ran the analysis five times on different subsets by randomly sampling different observations from the same pair. For all model coefficients and significance values we present mean value from the five analyses.

We also used a paired approach which enabled us to control for differences among individuals, or nest location, to assess whether the sexes responded differently to variation in modelled egg temperature. This method enabled us to detect interactive effects between sex and temperature. In the two years we conducted more than one incubation observation from 43 nests. We compared the nest attendance between the highest and lowest modelled egg temperatures observations from repeated observations of the same clutch. We only included one set of paired observations for each breeding pair of plovers. We conducted a Wilcoxon's signed rank test of related samples to examine differences between male and female nest attendance for the paired nest observations.

The above analysis can only be used to assess how the rank (i.e. lower [Lr] or higher [Hr] temperature) in paired observations affects male or female attendance. Absolute temperature (T_{La} and T_{Ha} for low and high absolute temperatures, respectively) is likely to affect the difference in attendance between the two observations. We divided the 43 paired observations into two groups on the basis of the modelled egg temperature from the higher observation of each pair (> 36°C or ≤ 36°C). There were 21 and 22 pairs in the low [La] and high [Ha] temperature category. The mean difference between the Lr and Hr of each pair was independent of the absolute temperature ($[T_{LrHa} - T_{HrHa}] - [T_{LrLa} - T_{HrLa}] = D_T = 0.98 ± 0.57$°C, $T_{41} = 1.6$, $P = 0.10$). We ran a Wilcoxon's test of related samples for the two absolute temperature categories (Ha and La) separately. We also tested to see whether absolute temperature category affected the difference between

attendance of the sexes at the low and high temperature pairs ($[AM_{Lr} - AF_{Lr}] - [AM_{Hr} - AF_{Hr}]$ at Ha or La).

For each observation on chick-rearing plovers, we calculated the percentage of scans in which males and females spent feeding, defending territories, and responding to disturbances or watching for predators. We also calculated a mean chick-to-adult distance for each observation period. Any repeated observations from the same brood in a year were averaged and this mean value was used for the subsequent test. We ran a Wilcoxon's signed ranks test of related samples to assess whether the frequencies of different behaviour and chick-to-adult distances differed between mates of the same pair. Between the two years, 11 pairs managed to double-brood, we did not conduct any repeated observations on the same pair at different nests. For this and subsequent analysis from observations of chick-rearing adults, we ensured that we did not resample the same individual between the two years by only including individuals that were colourbanded at the end of the 2004 breeding season and not sampled in 2005, along with all individuals from 2005. It was reasonable to assume that no birds lost all four bands (three darvic and an aluminium band) between 2004 and 2005. For chick-rearing adult observations 44 different pairs were sampled between the 2 years.

To test the effect of chick age on the prevalence of behaviour and adult-to-chick distances, we only included the broods for which we had replicate samples for the same breeding attempt at different chick ages (120 observation periods of 33 broods). We created two categories on the basis of chick ages (less than 15 days old or greater than 15 days old). For each of the 33 broods we calculated mean frequencies for territorial behaviour, vigilance, and feeding, and mean adult-to-chick distances for the two age categories. We compared the behaviour frequencies and distances between the two chick age categories for males and females using a Wilcoxon's signed ranks test of related samples.

Using a chi-square analysis we tested whether chick age affected the frequency of biparental defence chick defence, male-only defence, and female-only defence for the 71 disturbance watches (39 pairs) in which a potential predators or a neighbouring conspecific disturbed chicks. For this analysis we pooled data from broods 1 and 2 weeks old and also from broods 3 and 4 weeks old to increase the number of observations in each category. If there were multiple disturbances in a brood watch, we used the most frequent type of response during the entire observation period for the analysis.

To examine the potential fitness benefits of defending territories, we used a binary logistic regression to determine whether the percent of scans in which male or female plovers spent time defending territories from conspecifics affected the likelihood of fledging at least one chick. In total, 54 and 83 chick-rearing adult observations were conducted at 22 and 34 different breeding attempts in 2004 and 2005, respectively. We used mean values of territoriality for replicate watches from the same breeding attempt and we did not sample the same brood at different nests in the same year. Between the two years we obtained both breeding success and behavioural observations from at least 44 different pairs of plovers. The potential reproductive benefits of territorial behaviour may depend partly on the density of other Malaysian plover nests. Thus we statistically controlled for breeding density (number of nests within 200 m of nest site using GPS coordinates) and year by including it in the logistic model (Hosmer and Lemeshow 2000).

Differences between habitat quality could confound results on the effect of territorial behaviour on breeding success. Results from aprevious study on habitat-specific breeding success suggested that 0.5–5 m tall vegetation behind the beaches provides cover for Malaysian plover chicks and enhances fledging success (Yasué and Dearden 2006c). Consequently, we also visually estimated percentage cover of 0.5–5 m tall vegetation along three 50-cm-wide transects running perpendicular to the tideline and extending 20 m into the vegetation from the beginning of the vegetation line on the upper shore of the beach (Daubenmire 1959). This measure of percentage vegetation cover was also included in the logistic model to predict fledge success.

For focal observations, behavioural data (time budgets) were standardized to percentage time. In total 1,291 focal observations were conducted on plovers at different breeding stages during the two years. To reduce pseudoreplication, however, we calculated mean values for each individual in each of the four breeding status categories for each year. For any individual in which we had multiple values for different breeding statuses or years we randomly selected one sample. We excluded observations from unbanded birds. We obtained 71 and 80 focal observations from banded male and female plovers and this included 33, 14, 18, and 15 observations from adult plovers that were known to be pre-breeding, inactive, incubating eggs, or rearing-chicks. We did not record breeding status for all individuals for which we conducted focal observations. We used a Kruskal–Wallis test to assess whether there were any differences between the time spent defending

territories, responding to disturbances, or feeding rates because of breeding status for each sex. If breeding status affected behaviour, we tested to see if there was any difference between the sexes separately for different breeding status categories. We used a Mann–Whitney test of independent samples to determine whether sex affected the prevalence of any of this behaviour.

All error bars in figures denote standard error.

Results

Pre-breeding season

At all five locations there were, on average, more males than females in the pre-breeding flocks (males 6.5 ± 0.84; females 4.8 ± 1.0 individuals). This effect was not statistically significant, however, probably because of the small sample size and statistical power (*Paired t-test* on log-transformed data $t_4 = 2.6$, $P = 0.063$).

These dense flocks had 6–51 individuals and were located within five 100–200 m wide beach sections. The larger flocks tended to occur at high tide in the early winter months (November–January). In February and March the flock sizes decreased as pairs dispersed and began to defend territories at nearby beaches. Sixty-eight percent of the 54 colour-banded birds that were captured in winter flocks at these three beach sections in 2003 later bred within 1 km. Of these 54 birds eight did not breed within the study area in 2004, but returned to breed in 2005. The beach sections where birds roosted had the highest nesting densities and earliest clutches and thus seemed to be high-quality breeding areas.

Incubation observations

Females incubated the eggs for a greater proportion of the observations than males (males = 0.26 ± 0.028, females = 0.41 ± 0.033 proportion of total nest observation, Wilcoxon's signed ranks test of related samples $z = -3.2$, $P < 0.001$, $n = 80$ nest observations). On average, the nest was incubated for 0.67 of the observation period, and both sexes participated throughout the incubation period.

Nests were more likely to be incubated during hot weather (binary logistic regression final model coefficients: $\chi^2_1 = 8.8 \pm 1.2$, $P = 0.006 \pm 0.003$, $n = 82$, factor coefficients: $b = 0.26 \pm 0.02$, Wald = 7.3 ± 0.9, $P = 0.010 \pm 0.004$, receiver operator characteristic area under curve ROC AUC = 0.72 ± 0.01; Fig. 1). For this
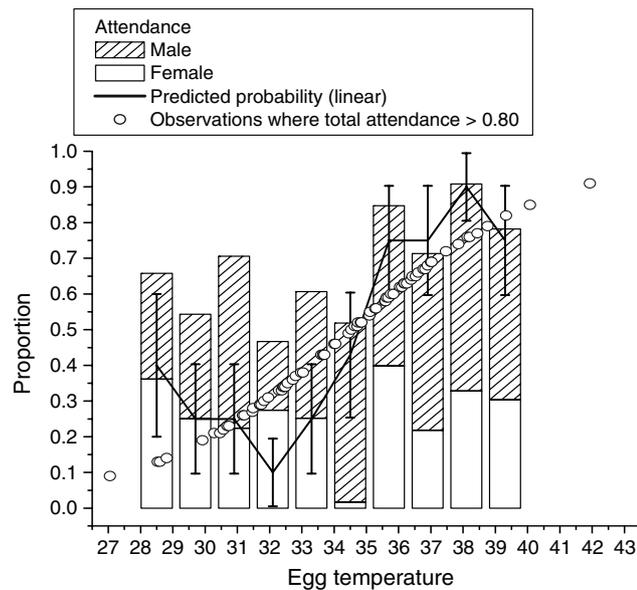
Fig. 1 Total nest attendance was greater at higher modelled egg temperatures. The *black line* represents the proportion of incubation observations where total nest attendance was greater than 0.80 for each temperature category. Sample size for each temperature category ranged from 5 to 10 and total sample size was 82. Shown also are *binomial error bars*. The *stacked bars* show male and female attendance and the *tops of the stacks* represent observed total nest attendance. *White circles* represent the fitted logistic regression curve showing the predicted probabilities from the model. The *bar graph* and the *logistic curve* are plotted on the same scale

and subsequent analyses, we did not include the quadratic term in the final model because it was not significant when we included both the linear and quadratic terms in the models. Crab burrow relative density ($P = 0.88 \pm 0.02$), embryo age ($P = 0.80 \pm 0.01$), and time of day ($P = 0.50 \pm 0.02$) had no effect on total nest attendance and were removed from the original model.

Male nest attendance was not affected by modelled egg temperature ($P = 0.32 \pm 0.05$). Egg temperature had a weak affect on female attendance ($\chi^2_1 = 3.5 \pm 0.19$, $P < 0.062 \pm 0.008$, $b = 0.17 \pm 0.009$, Wald $= 3.3 \pm 0.2$, $P = 0.061 \pm 0.011$, ROC AUC $= 0.63 \pm 0.001$). Crab burrow relative density ($P = 0.95 \pm 0.01$) and embryo age ($P = 0.952 \pm 0.001$) had no effect on the male contribution to nest attendance. Female attendance was not affected by egg temperature ($P = 0.51 \pm 0.02$), crab burrow relative density ($P = 0.45 \pm 0.04$), or embryo age ($P = 0.36 \pm 0.01$).

On the basis of the 43 paired observations of the same clutch at the highest and lowest modelled egg temperatures, female attendance (nest attendance for Lr and Hr: 0.35 ± 0.05, 0.53 ± 0.04, $z = -1.15$, $P = 0.25$) and total attendance (0.66 ± 0.05, $0.84 \pm$ 0.03, $z = -3.05$, $P = 0.002$) was affected by egg temperature but male attendance was not (0.31 ± 0.05, 0.31 ± 0.04, $z = -1.15$, $P = 0.250$). When we split the data into two categories on the basis of the higher temperature and re-ran the analysis, temperature had an effect on male and total attendance only when temperatures were greater than 36°C (Fig. 2). Females adjusted attendance at both high and low temperatures. There were statistically significant differences between attendance of the sexes for the high and low temperature pairs when modelled egg temperature was less than 36°C ($[AM_{Lr} - AF_{Lr}] - [AM_{Hr} - AF_{Hr}]$, $z = -2.31$, $P = 0.021$) but not at high temperatures ($T_{Ha} > 36°C$, $z = -0.016$, $P = 0.987$).

Brood observations

For the 44 different pairs of plovers males devoted a greater proportion of their time to territory defence and were significantly further away from chicks (males 0.08 ± 0.005, females 0.04 ± 0.008, $z = -2.97$, $P = 0.004$; and males 15.0 ± 1.11 m, females 13.3 ± 2.4 m, $z = -2.46$, $P = 0.014$, respectively). There was no significant difference between the time males and females spent feeding, responding to disturbances, or watching predators (males 0.14 ± 0.02, females 0.14 ± 0.02, $z = -0.47$, $P = 0.64$; and males 0.61 ± 0.03, females 0.59 ± 0.04, $z = -0.41$, $P = 0.68$, respectively).

For the 33 matched paired observations of the same brood at different chick ages, males were further from chicks when the chicks were older ($z = -2.5$, $P = 0.012$; Fig. 3). Chick age had no effect on female chick-to-adult distances ($P = 0.35$). Chick age had no statistically significant effect on the amount of time males or females spent feeding (males and females $P = 0.17$ and $P = 0.61$), defending territories ($P = 0.13$ and $P = 0.15$), or exhibiting disturbance behaviour ($P = 0.13$ and $P = 0.98$).

Both adults defended chicks during most human or predator disturbances. Chick age did not affect the frequency of biparental (64% of 39 disturbances of different pairs), male-only (12.8%), or female-only (17.9%) disturbance responses ($\chi^2_3 = 1.59$, $P = 0.662$, 24 and 15 samples were taken from chicks less than 15 days old or greater than 15 days old, respectively). We could not assess whether the type of parental response affected the success of nest defence from predators because there were very few diurnal predation attempts.

When we controlled for the number of conspecific nests within 200 m, percentage cover of 0.5–5 m tall vegetation, and year, both male and female territoriality contributed to greater breeding success (binary logistic regression for 44 different pairs, male complete

Fig. 2 The effect of modelled egg temperature on male and female attendance at temperatures less than (*left*) or greater than (*right*) 36°C. Males only adjusted attendance according to temperatures during hot weather. The furthest two vertical lines (F–M in the *X*-axis) represent the mean difference between the sexes for each Lr and Hr pair
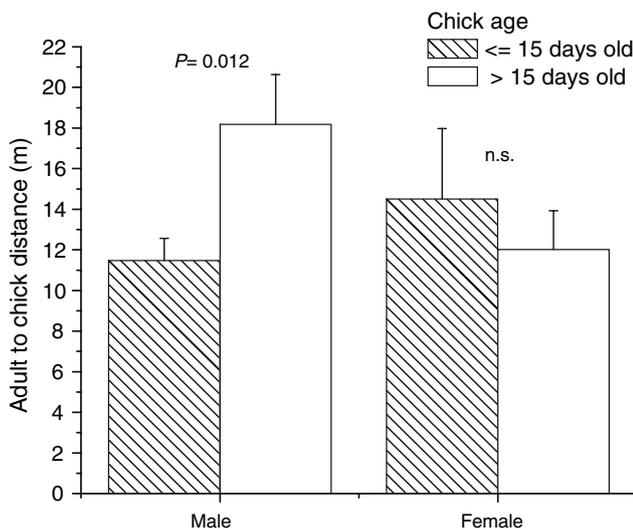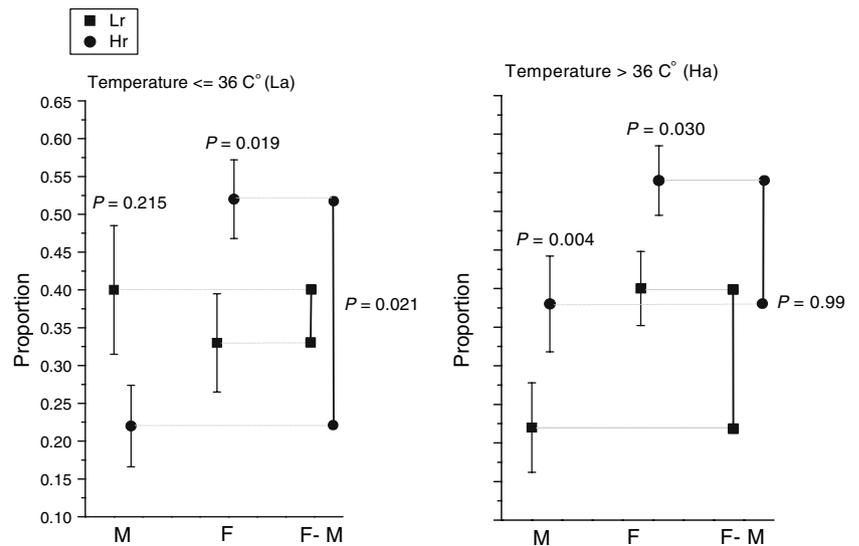

Fig. 3 The effects of sex and chick age on distances between adults and chicks

model coefficients: $\chi^2_4 = 11.0$, $P = 0.027$, factor coefficients with only significant variable: male $b = 26.2$, Wald = 7.8, $P = 0.005$, ROC AUC = 0.81; female complete model coefficients: $\chi^2_4 = 10.3$, $P = 0.036$, factor coefficients with only significant variable $b = 32.9$, Wald = 7.0, $P = 0.008$, ROC AUC = 0.78; Fig. 4). Neither conspecific nest density, percentage cover of vegetation, nor year had significant effects on fledging success.

Focal observations

Breeding status affected the number of feeding attempts for females (Kruskal–Wallis test, $\chi^2_3 = 14.6$,

$P = 0.002$, $n = 70$, pre-breeding season [1.73 ± 0.46], pairs without nests or chicks [1.72 ± 0.46], incubation [5.11 ± 1.43], or chick-rearing [0.84 ± 0.36]). Breeding status had no affect on the number of feeding attempts for males ($\chi^2_3 = 6.33$, $P = 0.096$). Breeding status had no effect on the total amount of time either of the sexes spent responding to disturbances (males $\chi^2_3 = 5.3$, $P = 0.15$; females $\chi^2_3 = 6.4$, $P = 0.09$) or defending territories (males $\chi^2_3 = 0.91$, $P = 0.82$; females $\chi^2_3 = 2.2$, $P = 0.54$).

Males spent more time defending territories than females (males 2.2 ± 0.4% time, $n = 80$; Females 0.83 ± 0.4% time, $n = 70$; *Mann–Whitney test of independent samples* $z = -2.6$, $P = 0.013$). Territorial interactions occurred between males, males and females, and females only. There were no significant differences between the number of feeding attempts for the sexes (males 1.7 ± 0.29, females 2.3 ± 0.39 attempts min^{-1}; pre-breeding season $P = 0.640$, pairs with no nests or chicks $P = 0.754$, incubation $P = 0.97$, or during chick-rearing $P = 0.060$), or disturbance behaviour (male 1.34 ± 0.34, female 0.95 ± 0.29 s min^{-1}; $z = -0.72$, $P = 0.47$).

Discussion

This is the first detailed study of parental care of Malaysian plovers and one of the few studies examining how environmental factors affect the breeding behaviour of a tropical shorebird. Our study adds to research on shorebird breeding ecology by quantifying behavioural differences between sexes from the non-breeding season in November to the chick fledging period in July

Fig. 4 Pairs that spent more time defending territories had a greater chance of fledging at least one chick (controlling for conspecific nest density and percentage cover of 0.5–5 m tall vegetation; $n = 40$ pairs). Bars represent the proportion of clutches that fledged at least one chick in each territorial behaviour category. For the highest category of territorial behaviour we pooled all higher values so the sample size was sufficient ($n > 4$) in each bar. *Binomial error bars* are shown. *White circles* represent the fitted logistic regression curve showing the predicted probabilities from the model. The *bar graph* and the *logistic curve* are plotted on the same scale
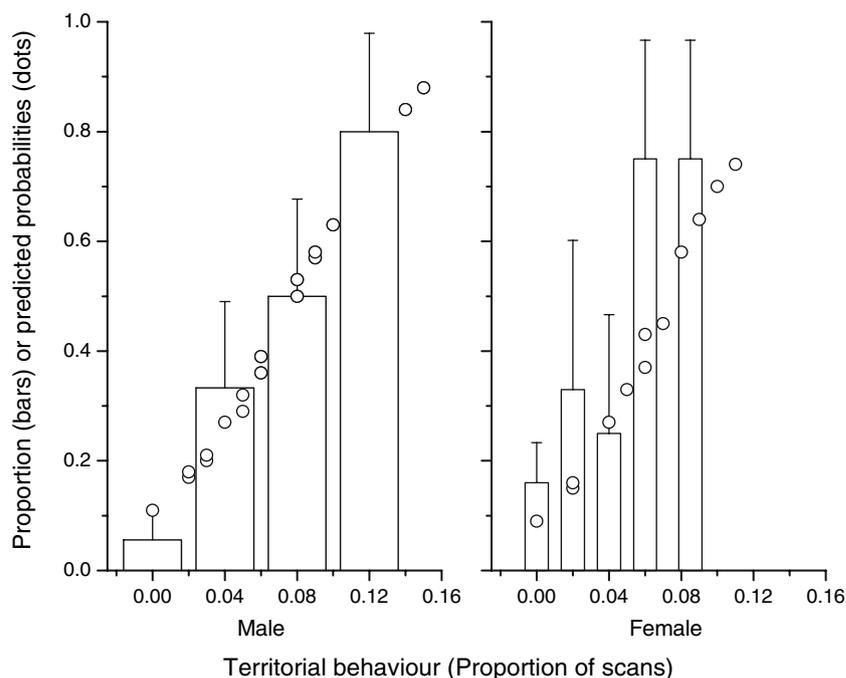
and assessing how chick age and environmental factors affect the partitioning of parental duties.

The main differences between the sexes were that females contributed more to diurnal incubation whereas males contributed more to territorial defence.

Malaysian plovers shared parental duties throughout the entire breeding season and there was no indication that the egg-laying costs for females or lower parental certainty for males resulted in significant differences between overall parental effort. Both sexes built nests, incubated clutches, defended territories, and protected chicks from predators throughout the entire breeding period. This type of biparental care between the sexes occurs for some *Charadrius* plovers (Wallander et al. 2001), and other studies have revealed greater role division and desertion of clutches or chicks by one of the sexes (Walters 1982; Warriner et al. 1986; Székely and Cuthill 1999).

Females did not have higher feeding rates than males, and there was no detectable increase in male territoriality before egg-laying. This suggests that compared with some other shorebirds (Székely and Lessells 1993; Oring et al. 1994), both female energy constraints and risk of cuckoldry for males may be less important factors shaping Malaysian plover breeding strategies than for other shorebirds.

Female energy constraints

Female Malaysian plovers may not have difficulty acquiring and replenishing energy reserves to lay eggs,

because our study population had biparental incubation, relatively low incubation requirements for clutches, and high and stable diurnal prey availability (Yasué 2006). Even females nesting in areas of low prey availability probably had sufficient time to meet energy requirements without reducing nest attendance, because nests were rarely incubated during cloudy periods or after 16:00 in the afternoon. Total Malaysian plover nest attendance (67%) was low compared with that for other, related, plovers, for which diurnal nest attendance is usually above 80% and greater than 90% for species with biparental incubation (Norton 1972; Thibault and McNeil 1995; Kosztolanyi and Székely 2002; Wallander 2003). Malaysian plovers probably had low nest attendance because incubation was not necessary for eggs to remain within the optimum temperature range during most of the day. From late May to July in the Gulf of Thailand it is cloudy in the afternoon and diurnal temperatures with cloud cover usually ranged between 33 and 37°C (Appendix).

The value of territorial behaviour

Our study suggested that territory defence by both mates increased the chance of chick survival. Males also defended territories throughout the entire pre-breeding and breeding season and did not increase territorial defence efforts during periods when the risk of EPC was higher. These results suggest that male territorial defence should be regarded as *parental* (rather than *mating*) effort and that mates shared the

fitness benefits of this behaviour. Territory defence probably improves breeding success because neighbouring plovers repeatedly chase and attack Malaysian plover chicks. Aggressive neighbours prevent chicks from feeding on the mudflats and seem to restrict chicks to less productive beach habitat that are closer to vegetation where chicks can hide when attacked by conspecifics (Yasué, unpublished data). This type of aggressive conspecific behaviour has been observed in other plover species (Fraga and Amat 1996; Teoh and Weston 2002; Weston and Elgar 2005a).

In addition to these immediate threats of conspecifics on chicks, for long-lived birds, with high site fidelity and multiple broods in a single season (Yasué and Dearden 2006a), losing a territory during the breeding season may have significant costs to future reproductive success. Maintaining the size of territories and preventing conspecifics from stealing territories is also particularly important for our study population because recent coastal development projects have dramatically reduced the amount of suitable Malaysian plover breeding habitat (Yasué and Dearden 2006c). Higher breeding densities that occur as a consequence of reduced habitat availability can cause prey depletion or enhanced nest predation and lower breeding success (Page et al. 1983; Sutherland and Anderson 1993). Despite favourable energy conditions for females to re-nest, relatively low required incubation effort, and low nest or chick predation (Yasué 2006), neither the male nor female abandoned clutches to re-nest with a different mate. Limited availability of high-quality breeding habitat may be an important factor contributing to biparental care and mate retention (and thus habitat retention) throughout the breeding season.

Complementary sex roles

Behavioural differences between the sexes could be largely because of efficient allocation of parental duties, based on the different abilities in the sexes, for mutual gains. For example, plumage colour may be an important difference between the sexes because plovers nest on sandy white beaches and both their nest and chicks rely largely on crypsis to reduce predation risk (Kosztolanyi and Székely 2002). During the day female Malaysian plovers may contribute more to nest incubation and remain closer to chicks because predators are less likely to see females. Previous studies on related plovers (Fraga and Amat 1996; Kosztolanyi et al. 2003) also revealed higher female diurnal nest attendance.

It is also possible that females spend more time incubating nests or remaining close to chicks because males are better at defending chicks from conspecifics (Fraga and Amat 1996). Although male and female plovers do not differ in body size (Yasué 2006), there could be other dissimilarities between the sexes, for example testosterone levels, flight speeds, or colour markings that could affect territory defence ability (Graul 1973). In contrast to females that remain close to chicks near the beach, males often watched chicks and beach habitats from the mudflat. By having a wider vantage point males may be more able to detect distant approaching predators and alert the more camouflaged females who can quickly lead chicks into the vegetation behind the beach and also defend both mudflat and beach segment of territories from conspecifics.

Alternatively, females may incubate more during the day because males are better able to incubate at night (Jehl 1973; Warnock and Oring 1996; Kosztolanyi and Székely 2002). Male-biassed nocturnal incubation has been documented in many studies (reviewed by Wallander 2003). These authors suggested that females incubate more during the day so that females can recoup body condition (Wallander 2003) by feeding at night when there are fewer human disturbances (Burger and Gochfeld 1991) or higher prey densities (Turpie and Hockey 1993). This may not be an important reason for female-biased diurnal incubation, because of the low incubation requirements of clutches (as discussed above) and low diurnal human disturbance rates at our study sites (Yasué and Dearden 2006c). Their main prey, *Scopimera* crabs, are, moreover, more abundant in the early afternoon than at night (Yasué unpublished data; Zwarts 1990).

Previous studies have also suggested that male nest attendance increased during periods of adverse weather (Norton 1972). Male Kentish plovers and common ringed plovers both contributed to only a small percentage of diurnal incubation, and restricted these efforts to the hottest hours of the day (Wallander 2003; Amat and Masero 2004). Malaysian plovers frequently cooled legs and bodies in pools of water before and immediately after incubation bouts. Although females played a greater role in regulating egg temperatures, during particularly hot periods male Malaysian plovers incubated nests and prevented excessive heat stress that could impair female body condition and reduce hatch success (Ward 1990; Amat and Masero 2004).
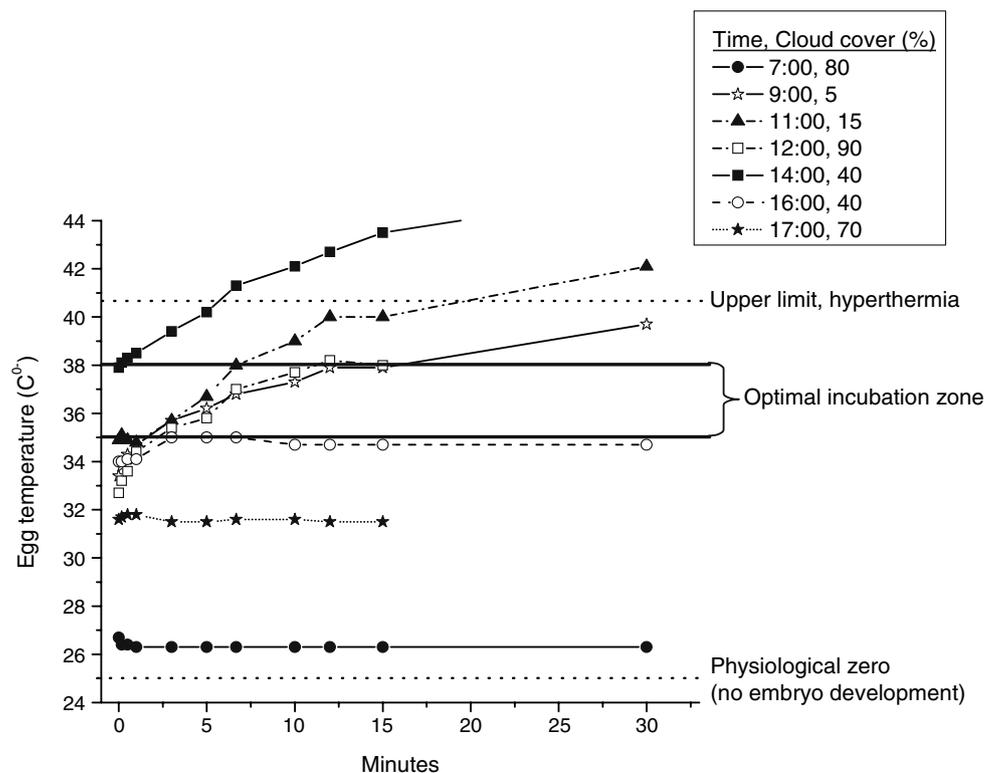
Future research

Genetic fingerprinting to determine paternity would have improved the explanatory power of our study. On the basis of behavioural observations in our study it seems EPC may be quite low for Malaysian plovers. They had biparental care, social monogamy throughout

the entire breeding season, low copulations rates [0.18 copulations h^{-1}, $n = 501$ focal samples, compared with previous studies (Birkhead and Møller 1996; Pierce and Lifjeld 1998; Wallander et al. 2001)], and we did not observe any EPCs, or mate guarding. EPCs could occur at night, however (Double and Cockburn 2000; Johnson et al. 2002).

Nocturnal studies on territoriality, foraging efficiencies, and incubation duties are also important for comparing parental effort and better understanding the ecological factors contributing to the different behaviour of the sexes (Kosztolanyi and Székely 2002; Wallander 2003). Although we detected changes in male incubation behaviour during the day, 24-h studies are necessary to evaluate whether males increase parental effort, or if males increase diurnal parental care because females increase nocturnal incubation effort.

In this study we compared time budgets between sexes. To compare the complete costs of parental care and reproduction between sexes, however, it would be important to measure and compare the energy cost of egg production with the field metabolic rate of several types of behaviour, for example territory defence, to measure cumulative energy expenditure (Nol 1985; Brunton 1988). Despite potential for differences between prey availability and energy considerations for tropical and Arctic species, very few energy studies have been conducted in tropical environments.

Conclusion

Malaysian plovers have strong competition for breeding territories, shared biparental care, high social monogamy, and high cooperation between the sexes. The restricted breeding habitat availability, long breeding seasons, productive and stable prey source, and warm weather conditions in the study environment may have contributed to this parental behaviour. A better understanding of how environmental and ecological conditions affect the fitness-maximizing decisions of tropical species may lead to a more complete analysis of the evolution of avian breeding systems and mating strategies.

Appendix. Egg temperature model

Figure 5 shows the increase in temperature inside quail eggs placed in a disused Malaysian plover nest cup as a

Fig. 5 The effect of time of day, percent cover (see legend) and minutes of exposure (x-axis) on the temperature inside quail eggs placed in disused Malaysian plover nest cup

function of minutes of exposure to sunlight and to cloud cover at different times of day. On most days cloud cover was sufficiently high, or air temperature sufficiently low, that unshaded eggs remained within the upper and lower limits for incubation. As illustrated by the black squares and triangles, however, on particularly hot days, egg temperatures can quickly exceed the upper limit for hyperthermia for embryos.

$$T_{egg} = -12.86 + 0.906 \times T_{sa} - 0.345 \times C \\ + 3.57 \times H - 0.143 \times H^2$$

where T_{egg} is the temperature inside the egg after 15 min of exposure, T_{sa} is the shaded ambient temperature, C is the percentage cloud cover, and H is the time of day (h).

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