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Replacement nesting and double-brooding in Malaysian Plovers *Charadrius peronii*: effects of season and food availability

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In shorebirds, the prevalence of successive clutching and types of associated breeding strategies differ among species, environments and individuals. Although several studies have examined successive clutching behaviour in holarctic species, little research has been conducted in the tropics. To assess the full range of reproductive strategies and better understand breeding constraints in tropical environments, we characterised successive clutching behaviour in 54 and 79 colour-banded Malaysian Plovers *Charadrius peronii* over two years in the Gulf of Thailand. We also examined monthly changes in clutch size, clutch volume, prey availability and breeding success because temporal variability in breeding conditions can affect the prevalence, timing of, and parental role-division between successive clutches. Short intervals between clutches, successive monogamy, high within-season site fidelity, double-brooding, and complete biparental care were general characteristic of successive clutching behaviour. We did not detect any declines in clutch size, clutch volume, prey availability and reproductive success during the course of the breeding season. For Malaysian Plovers, the stable and progressively favourable prey supply and weather conditions, lack of migration, and intense competition for breeding habitats may have contributed to a breeding system constrained more by habitat availability than by time. In these environments, pairs may retain mates and breed multiple times during the long breeding season.

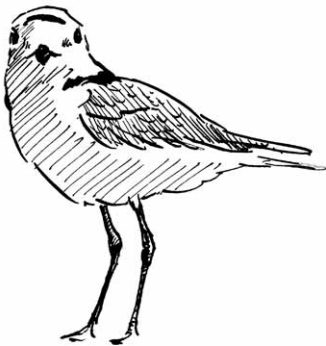
Key words: breeding, successive clutching, mating strategy, shorebird, parental care

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INTRODUCTION

Shorebirds are an ideal taxon to examine the evolution of mating strategies and variation in parental care behaviour because of their highly variable breeding strategies (Reynolds 1996, Blomqvist *et al.* 2001, Székely *et al.* 2006). Part of this variability is a consequence of adaptations to different ecological and physical conditions (Székely & Cuthill 2000). Although numerous studies have focused on the breeding ecology of temperate and arctic shorebirds, more research is needed to understand the full range of variability in shorebird breeding behaviour and to identify the environmental constraints that shape breeding behaviour in tropical species (Thomas *et al.* 2003).

Successive clutching (re-nesting) occurs when birds lay clutches after *failed* attempts ('replacement clutching') or try to fledge more than one brood in a single season ('double-brooding'). The prevalence of successive clutches, timing of successive clutches, parental role divisions, and mate or site fidelity between clutches vary both across and within shorebird species (Blomqvist *et al.* 2001, Andersson 2005). The contrasting environmental conditions in holarctic and tropical areas may lead to differences in successive clutching behaviour between closely related holarctic and tropical shorebirds (Johnsgard 1981, Martin 1996).

A key difference between holarctic and tropical environments is the degree of seasonal variability in shorebird prey abundance. High latitude environments are characterised by a brief burst of high prey availability followed by a progressive decline in productivity (Graul 1976, Pitelka 1979, Breiehagen 1989, Smith *et al.* 1989, Sandercock *et al.* 1999). In these types of time-constrained environments, females may exhibit sequential polyandry or may rapidly lay successive clutches ('multiple-clutching') during periods of high productivity (Oring & Knudson 1972, Breiehagen 1989). The condition of females breeding at high latitudes may decline later in the breeding season and, as a result, they may be more likely to desert clutches, contribute less to parental care, or produce smaller clutches or eggs than those in the tropics

(Rooneem & Robertson 1997, Sandercock *et al.* 1999). Near the beginning or end of the breeding season there could be cold weather periods and females may also have greater difficulties meeting the higher energetic demands for thermoregulation at higher latitudes and could thus take more time to lay successive clutches (Nilsson & Svensson 1996, Amat *et al.* 1999b, Amat *et al.* 2000, Blomqvist *et al.* 2001).

In contrast to holarctic shorebirds, tropical species may have longer breeding seasons because of extended periods of favourable weather and a more stable prey base (Johnsgard 1981, Martin 1996). Longer breeding seasons could lead to greater replacement clutching (successive clutches after failed attempts) and double-brooding rates (successive clutches after successful attempts) (Dowding *et al.* 1999). Moreover, female birds that have longer intervals between successive clutches would have more time to build or replenish energy reserves for egg laying.

Shorebirds may have partial or complete uniparental care by either of the sexes, sequential polyandry where the male may care for the first clutch while the female incubates the second clutch (Graul 1976, Erckmann & Wasser 1983, Breiehagen 1989, Blomqvist *et al.* 2001), or complete biparental care (Lenington 1980, Székely & Cuthill 1999). Many temperate or arctic species may have evolved polygamous mating systems with partial or complete uniparental care because of the relatively short breeding seasons (Graul 1976, Bergstrom 1988). Complete biparental care necessitates longer inter-clutch intervals because successive clutches are usually only laid after the fledge date of the primary clutch (Blomqvist *et al.* 2001). Nest desertion by one parent is adaptive for the deserting parent if the remaining parent is able to fledge chicks on its own (Amat *et al.* 1999a, Székely *et al.* 1999, Johnson *et al.* 2006). Thus complete biparental care of successive clutches and longer inter-clutch intervals may be favoured in environments where nests and chicks are moderately vulnerable to thermal stress, predators, or attacks from conspecifics, and the cooperation of both adults increases fledging success rates

(Erckmann & Wasser 1983, Dale *et al.* 1996, Reynolds & Székely 1997).

We examined successive clutching in a sedentary shorebird, the Malaysian Plover *Charadrius peronii*, a threatened species (IUCN redlist) that breeds in the Gulf of Thailand. We conducted behavioural observations and monitored breeding success to describe the successive clutching behaviour of Malaysian Plovers and assess whether food demand, temporal constraints, or parental care requirements may have shaped this aspect of their breeding ecology.

METHODS

Study area and population

From 15 November 2003 – 25 July 2004 and 10 January – 25 July 2005, we studied plovers along a 108-km section of sandy beaches in the Gulf of Thailand between Bornok Beach (12°00'N, 99°53'E) in Prachuap Khiri Khan Province and Laem Phak Bia (13°03'N, 100°05'E) in Petchburi Province, Thailand. During January and February, Malaysian Plovers began defending 100–300 m long, multi-purpose territories that included an intertidal mudflat foraging area, a sandy beach for nesting, and a shrubby, vegetated area behind the beach that provided cover for chicks. The weather from April to May tends to be hot, humid, and sunny (diurnal temperature range 28–42°C). Later in the season, the weather becomes cooler, cloudier, and wetter (26–38°C).

Field observations

We monitored 86 and 126 nesting attempts of 54 and 79 pairs in 2004 and 2005, respectively. We used either noose mats (Mehl *et al.* 2003) or walk-in funnel traps (Székely *et al.* 2006) to capture most adults (65 and 70%) either during the preceding winter or during the 2004 and 2005 breeding seasons. We captured 118 adults and 88 chicks in 2004, and 75 adults and 103 chicks in 2005. We also captured and individually colour-banded chicks within two weeks of hatching and returned to the nesting territories every four to eight days for up to 30 days to assess chick survival.

During the breeding season, we surveyed beaches and mudflats for Malaysian Plovers. Nests were located by searching areas where pairs were observed and by watching birds return to nests. We visited nests every three to five days to detect embryo mortality, estimate laying, and hatch dates (by floating eggs), based on a 30-day incubation period and initiation of incubation after the laying of the first egg (Westerkov 1950, Powell 2001, Yasué & Dearden 2006a). When nests or broods disappeared between checks, we recorded the date of nest failure as the median date during the interval between nest checks (Mayfield 1961). Close to the predicted hatch date, nests were checked daily because of the high mortality rates of newly-hatched young. We were able to discriminate between failed and successful nests because: 1) chicks remained within 200 m of nest sites, 2) chicks could be observed from a vantage point on the mudflat, and 3) adults with chicks performed conspicuous displays whereas adults without chicks spent most of their time feeding and roosting on the mudflat and beach. When nests failed we conducted extensive observations of the pair and recorded behaviour such as mate guarding, nest building, or copulation to determine whether pairs laid successive clutches.

Throughout the breeding season we surveyed 15 beaches within 3 km once per month where plovers were not observed in the winter or during the early part of the breeding season to ensure that we did not miss re-nesting attempts by banded birds that may have changed territories. Monthly surveys were sufficient to identify new nesting territories because plovers occupied territories for several weeks to months prior to nesting and remained in territories throughout the tidal cycle even prior to nesting or after failed breeding attempts.

We defined the re-nesting interval for replacement nests as the number of days between nest failure and the date the first egg of the next clutch was laid. For pairs that attempted to raise more than one brood in a season (i.e. double-brooding; Blomqvist *et al.* 2001), we calculated the interval between nests as the number of days between the

fledge date of the first nest and the date the first egg of the nest clutch was laid. Brood overlap was the number of days in which adults cared for the unfledged chicks of the first clutch and also incubated nests of the successive clutch at the same time. Fledge date ranged from 27–33 days. We determined fledge date by observing short distance practice flights or flushing chicks to force them to fly.

We may have underestimated the proportion of pairs that successively nested because our study ended before the end of the breeding season and nests in the past have been documented until at least the end of July (Summer-Smith 1981) and local fishers suggested that nests have been observed in September (C. Wataksorn, pers. comm.). However, we found fewer nests in late June and July, and the peak egg-laying period was during late April and early June (Fig. 1).

We measured the maximum length and width of eggs (± 0.1 mm) using calipers. We calculated egg volume (V) from maximum egg width (W) and length (L) using the formula used by Fraga & Amat (1996) for the eggs of the closely related and similar-sized Snowy Plover *Charadrius alexandrinus* (Robson 2002):

$$V = \left[0.5236 - \frac{0.5236 \times 2 \times L}{W \times 100} \right] \times L \times W^2$$

If females re-nested more than once in a season and we were able to record clutch size and egg volume for all nests, we compared the mean clutch size and egg volume of successive clutches to those of the earliest recorded nest.

Observations of parental care

We observed adults with nests and broods randomly throughout the day between 6:30 and 17:30 in 2004 and 2005. Repeat nest and brood observations on the same pair were conducted on different weeks and no more than three times per breeding attempt (cumulative for nests and brood watches). One to two-hour observation periods (mean 75.7 ± 2.3 min, 211 observation periods) during incubation ($n = 113$ nests) and 45–60 min

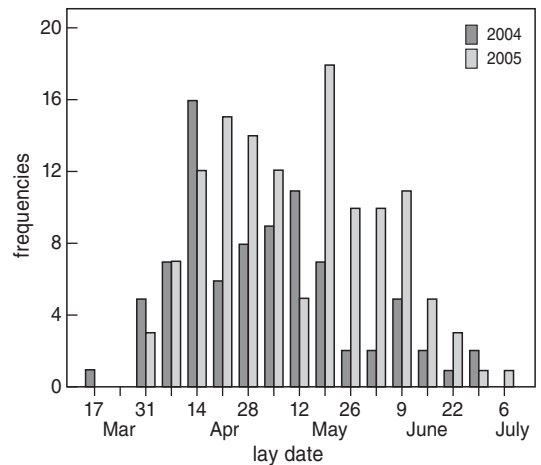


Figure 1. Frequencies of lay dates of Malaysian Plover nests in 2004 and 2005.

observations (mean 50 ± 1.3 min, 134 observation periods) of pairs with broods ($n = 57$ broods) were conducted from April–July. Between the years these observations were conducted on 95 and 54 pairs with nests or broods for a total of 163 and 109 hours. To minimize disturbances we observed birds using either a 15–45x spotting scope or 10x50 binoculars from a blind or a seated position on a mudflat more than 150 m from the plovers.

For each observation the sex of the incubating bird was recorded as well as the time when incubation bouts started and ended. During observation of broods, we conducted instantaneous scan samples (Boettcher *et al.* 1994) and recorded the behaviour of the chicks and both adults at 5-min intervals. In addition to incubation or brood observations, we also conducted 5–25 min long focal observations of adults (mean 8.0 ± 0.2 min, $n = 858$) to detect new pairings or territory changes. Adults were selected randomly and only sampled once a day.

Prey availability

Observations of adult plovers indicated that they fed on *Scopimera globosa* crabs 80% of the time. Therefore, on three beaches with nesting plovers,

we determined the density of *Scopimera* crab burrows once per month, between 11:00 and 13:30, from May–July 2005, and at the same stage in the tidal cycle. Samples were taken from the same 300 m length of beach for each of the three months to reduce the risk of confounding spatial and temporal variability. For each 300-m sampling section, we paced a transect perpendicular to the shore onto the mudflat and measured and paced the total width of the mudflat where crab burrows were present. Along each transect we sampled three crab burrow densities in 0.44 m² quadrates. Three to four transects were sampled at each beach for each sampling section. We multiplied the three crab burrow densities on a particular transect by the length of the mudflat that had crab burrows. Data were converted to densities per m² and log₁₀-transformed so that data approximated a normal distribution.

Breeding success and successive clutches

We examined hatching and fledging probability based on daily survival estimates (Mayfield 1961) for clutches laid in the early (before May 15), mid (15 May – 15 June) and late (16 June – July) periods of the breeding season. Time intervals were divided in this manner so that there was approximately the same number of nests in each date category. We calculated the number of failed or successful nests based on the daily survival rates of nests and chicks and used these data in a Chi-Squared test of Independence (Dow 1978). We defined breeding success as the probability that at least one chick fledged from a breeding attempt, nest success as the probability that at least one chick hatched, and fledge success as the probability that a successful nest fledged at least one chick. We combined nest and chick success probabilities to calculate an overall probability of 'breeding success'. In cases where there are substantially greater survival rates in different breeding stages this can lead to severely biased estimates of breeding success using the Mayfield's method (Mayfield 1961, Dow 1978, Johnson 1979). We were able to combine the two breeding stages for an overall breeding success assessment without biasing our results

because there was no significant difference in the length of the incubation (Wilcoxon's test of independent samples = 122, $z = 0.72$, $n = 21$; $P = 0.471$) and fledging period (Wilcoxon's test of independent samples = 97.5, $z = -64$, $n = 19$; $P = 0.522$) or between the survival rates of eggs or chicks in both years (2004: $\chi^2_1 = 2.0$, $P = 0.16$ and 2005: $\chi^2_1 = 1.4$, $P = 0.24$).

Statistical analysis

All data analysis was conducted using SPSS version 11.0 (SPSS 2001) and all error estimates presented in the text and figures are standard errors. Test results are two-tailed and based on significant levels of $\alpha = 0.05$.

We constructed different models for the two years instead of pooling different years because at least thirty-five of the pairs sampled in 2005 were also studied in 2004 and we needed to reduce pseudoreplication. We did not combine data from the two years and included 'individual' as a random factor because not all breeding pairs of plovers in 2004 were colour banded at the end of the breeding season. In addition there were significant differences in breeding success ($\chi^2_1 = 4.2$, $P = 0.04$) and changes in habitat quality due to the construction of new resorts and a seawall (Yasué & Dearden 2006b). We also sampled a larger area in 2005. If there was more than one nest laid by the same pair during the same time interval in each year, we randomly selected one of the nests.

Using binary logistic regression, we tested whether lay date of primary clutch and failure date of the primary clutch influenced the likelihood of re-nesting or double brooding. Although some plovers re-nested multiple times in a breeding season, we only examined the re-nesting 'decisions' after the primary clutch. This is because we did not monitor breeding plovers until the end of the breeding season. Secondary or tertiary re-nest attempts tended to occur later in the breeding season and there was a higher likelihood that we failed to detect re-nests due to the length of our field season.

For this analysis, we initially controlled for habitat characteristics that were shown to influence

breeding success in a concurrent study. These variables were human disturbance levels (based on censuses of dogs and humans on the beach), predatory *Ocypode* crab densities on the beach, and the number of conspecific nests within 200 m for 2004. The latter two variables were controlled for 2005. Human disturbance levels did not have significant effects on breeding success in 2005 (Yasué & Dearden 2006b). Insignificant habitat variables were sequentially removed. Lay date and failure date of the primary clutch were correlated to each other (2004: Pearson's correlation $r = 0.59$, $P < 0.0001$; 2005 $r = 0.64$, $P < 0.0001$) and could not be included in the same model. For this reason we constructed two models and assessed Receiver Operator Characteristic Curves (ROC) to evaluate which date variable best predicted re-nesting behaviour. For binary logistic regression, the area under a Receiver Operator Characteristic Curve (ROC) is a graphical depiction of the trade-off between a false positive and false negative rate, where 1.0 represents a model with 100% specificity and sensitivity and 0.5 is a model that is no better at predicting a binomially distributed value than chance (Zweig & Campbell 1993).

For all statistical analyses to examine seasonal changes in prey availability, clutch size, or egg volume, we used non-parametric tests if data were not normally distributed even after standard data transformations. For the analysis to assess whether there were seasonal changes in prey availability, data were first log-transformed and non-significant interaction terms were removed from the final model.

RESULTS

Successive clutches and inter-clutch intervals

Forty-one and 48% of the pairs in 2004 ($n = 54$) and 2005 ($n = 79$), respectively, re-nested (laid successive clutches) at least once during our study. Birds were more likely to re-nest if initial clutches failed compared to when birds fledged at least one chick ('replacement clutching' 2004: $\chi^2_1 = 7.1$, $P = 0.008$; 2005: $\chi^2_1 = 5.3$, $P = 0.021$, Table 1). The mean number of days between the loss of a nest and the laying of the first egg of the next nest was 9.8 ± 1.3 days ($n = 44$ pairs). In two cases, a second nest was initiated when there was still one surviving chick from the first nest (the chick from the first nest eventually died). One pair of plovers (both colour-banded) laid two clutches in a one week period 8 m apart and both adults contributed to the incubation of both clutches (Yasué & Dearden 2006a). Although only one of these two clutches hatched, this was the first documented case of biparental incubation and simultaneous successive clutching in a shorebird.

All five pairs that double-brooded in 2004 were colour-banded, but none of these pairs also double-brooded in 2005. Out of the 11 double-brooding pairs, nine pairs laid successive clutches before the chicks of the former nest had fledged. Adults divided their time between incubating the successive clutch and providing parental care for chicks of the primary clutch. On average there was 8.8 ± 3.7 days ($n = 11$) of overlap between successive clutches. The greatest overlap between successive clutches was 39 days. From 16 June (when the

Table 1. The percentage of Malaysian Plover pairs that laid successive clutches (SC) after successful (> 1 chick fledged) and failed initial breeding attempts in 2004 and 2005. The right-hand column gives the number of observed successive clutches per pair.

Year	Successful first nest		Failed first nest		Observed SC / pair		
	Total	% with SC	Total	% with SC	1	2	3
2004	24	21	30	57	16	4	2
2005	22	17	57	56	30	7	1

second clutch was laid) to 25 June (when the first clutch hatched) this pair incubated two nests 10 m apart, simultaneously. This pair fledged one chick from the first nesting attempt and hatched one chick from the second nesting attempt.

We did not determine if double-brooding increased breeding success because we were only able to measure fledging success in five (three of five successive nests failed) and three (all three successive nests failed) of the 11 double-brooding pairs in 2004 and 2005, respectively.

Site and mate fidelity

Fifty-three percent of the colour banded birds in 2004 returned to nest in our study area in 2005. However, actual adult survival was likely much higher because the significant changes in habitat quality that occurred between the two years are likely to have caused many birds to move elsewhere (Yasué & Dearden 2006b, 2008a).

Of 52 birds captured and banded in the winter of 2004, 38 did not breed in our study area (Table 2). The 14 banded individuals that remained throughout the winter and breeding season bred within 2 km, and on the same beach they were banded. During 6881 minutes of observations of adults during the breeding season, we observed

no extra-pair copulations and, other than territorial interactions with neighbours, adults were never observed outside of their own territories.

Of all successive clutches for 78 colour-banded plovers, only one individual re-nested in 2005 in a different territory. This male successively clutched 5 km away from its primary clutch with a different mate and the former mate was never observed again during our study. Excluding this individual, successive clutches were close to previous nests. In the 11 double-brooding individuals, pairs laid successive clutches in the same territories with the same mate. The fate of initial nesting attempts did not influence the distance between successive nests ($z = -1.0$, $P = 0.32$), with a mean distance of 60.3 ± 15.2 m ($n = 45$) between first and second nests after a failed nest and 92.3 ± 24.3 m ($n = 10$) after a successful nest.

There were 62 successive clutching attempts by 52 colour-banded pairs and only five re-nests involved mate changes between successive nests. Of these five successive clutches (three females and two males), one mate re-nested with a different partner within its original territory. These mate changes may have been caused by the death of a previous mate because we did not subsequently resight the former mate. For two of these successive

Table 2. Breeding site and mate fidelity of adult Malaysian Plovers that were colour-banded at nests in 2004 and returned to breed in 2005.

	<i>n</i>	%
Number of adults colour-banded during the 2004 winter	52	
of which breeding in study area	14	27
Number of adults colour-banded during the 2004 breeding season	56	
Colour-banded breeding adults at the end of the 2004 breeding season	70	
of which returning to nest in study area in 2005	36 ^a	51
Colour-banded pairs of plovers in 2004 (both male and female colour-banded)	32	
Both mates returned to breed in 2005 and:		
retained mates from 2004	16	50
paired with different mates	0	0
One mate returned to breed and mated with an unbanded bird	10	31
No pair members returned	6	19

^aAll 36 nested within 500 m of 2004 nest.

clutches, the individual that eventually switched mates initially remated with its former mate, and re-nested with a new partner only after their nests failed a second time.

Parental care

All but two pairs of Malaysian Plovers exhibited complete biparental care during incubation. At these two nests, one adult disappeared during incubation and nests were subsequently abandoned. During the chick-rearing period, both adults were present in their territories during all brood watches.

In brood watches conducted during the period when successive broods overlapped ($n = 5$), both parents contributed to both chick-rearing of the primary clutch and incubation of the successive clutch. In addition, we conducted two disturbance observations on pairs that were concurrently rearing chicks and incubating successive nests. In these two cases, the female remained on the nest while the male performed distraction displays.

Seasonal variation

Of 205 nests, 4, 20, 75, 0.5, and 0.5% had 1, 2, 3, 4, and 5 eggs, respectively. Clutch size and mean egg volume did not differ between the first and

second clutches of the same female (Table 3). For five pairs, we determined clutch sizes and egg volume for both initial nests and successive nests and found no differences in either clutch size (2004: $z = -1.9$, $P = 0.059$, 2005: $z = -1.0$, $P = 0.32$) or egg volume (2005: $z = -1.2$, $P = 0.23$).

For prey availability, the interaction term between site and season (in three categories) was not significant ($P = 0.21$) and was removed from the final model. Both season (Two-way ANOVA without interaction term $F_{2,96} = 14.5$, $P < 0.0001$) and site ($F_{2,96} = 10.4$, $P < 0.0001$, Fig. 2) had significant effects on crab burrow density. Crab samples were greater in June and July than in May (Tukey's test, mean difference May and June -0.31 , $P = 0.002$, May and July -0.47 , $P < 0.0001$).

We found no differences amongst the three time periods in overall Mayfield breeding success probabilities for either 2004 ($\chi^2 = 0.7$, $P = 0.72$, $n = 57$ clutches) or 2005 ($\chi^2 = 2.7$, $P = 0.26$, $n = 82$ clutches). We also found no differences among months in hatch and fledging probabilities (Hatch 2004 $\chi^2_2 = 2.6$, $P = 0.27$; 2005 $\chi^2_2 = 1.5$, $P = 0.48$; Fledge 2004 $\chi^2_2 = 1.3$, $P = 0.52$; 2005 $\chi^2_2 = 4.3$, $P = 0.12$, Fig. 3).

In 2004, both lay date of the primary clutch and date in which the primary clutch failed were

Table 3. Summary of clutch size and egg dimensions (mean \pm SE, n) and test results for the differences in clutch size (Wilcoxon's) and Paired t -test (volume) for first and successive Malaysian Plover clutches in the season.

	All observations	First clutch	Successive clutch	Test first–successive
Clutch size				
2004	2.8 \pm 0.07, 46	3.0 \pm 0.05, 19	2.8 \pm 0.07, 27	$z = 1.3$, $P = 0.19$
2005	2.7 \pm 0.07, 75	2.8 \pm 0.09, 32	2.7 \pm 0.07, 43	$z = -0.4$, $P = 0.71$
Egg width (cm)				
2004	2.36 \pm 0.04, 23			
2005	2.35 \pm 0.01, 70			
Egg length (cm)				
2004	2.92 \pm 0.04, 23			
2005	3.14 \pm 0.02, 70			
Egg volume (cm ³)				
2004	8.25 \pm 0.24, 23	8.16 \pm 0.45, 9	8.31 \pm 0.28, 14	$t_8 = -1.0$, $P = 0.34$
2005	8.86 \pm 0.11, 70	8.85 \pm 0.19, 28	8.90 \pm 0.14, 42	$t_{28} = -0.9$, $P = 0.35$

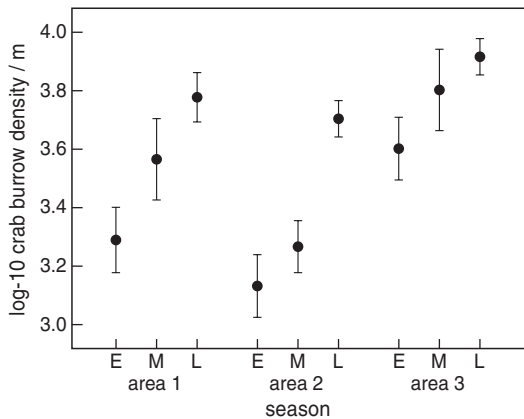


Figure 2. Seasonal (E = early before 15 May; M = 16 May – 15 June; L = after 15 June) abundance of *Scopimera* crab burrow densities at three 300 m long mudflats sections adjacent to Malaysian Plover nesting habitats in 2005. The three different symbols denote different locations. Between 9 and 12 density samples were taken at each site and time interval. Whiskers represent ± 1 SE.

significant predictors of whether or not a pair would renest (Lay date: $b = -0.86$, Wald = 11.3, $P = 0.001$, Model $\chi^2_1 = 20.3$, ROC = 0.84; Failure date: $b = -0.048$, Wald = 10.1, $P = 0.001$, Model $\chi^2_1 = 13.9$, ROC = 0.79). The ROC for lay date was slightly higher. In 2005, only failure date had a significant effect on the likelihood of renesting (Lay date: $b = -0.013$, Wald = 1.8, $P = 0.186$; Model $\chi^2_1 = 1.88$; ROC = 0.61; Failure date: $b = -0.034$, Wald = 8.5, $P = 0.004$, $\chi^2_1 = 9.7$, ROC = 0.71). The habitat variables were not significant ($P < 0.05$) and were dropped from the model.

DISCUSSION

As far as we know, this is the first detailed study on successive clutching in a tropical shorebird. Renesting after the loss of a nest, short intervals between replacement clutches, and frequent double-brooding have been documented for some species of southern hemisphere shorebirds (Summers & Hockey 1980, Pringle 1987, Pierce 1989, Weston 2000). Double-brooding occurs

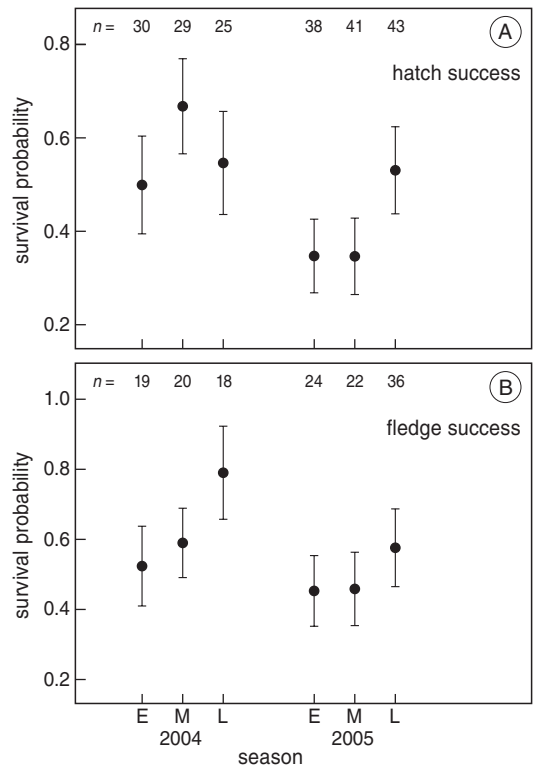


Figure 3. Seasonal variation in probabilities of hatching (A) and fledging (B) in Malaysian Plovers in 2004 and 2005. Success rates were based on daily survival estimates of clutches and chicks using Mayfield's (1961) exposure method. See Fig. 2 for explanation of seasonal periods. Whiskers represent ± 1 SE.

infrequently in holarctic environments (Wallander & Andersson 2003). The lack of seasonal declines in egg volume, clutch size, prey availability, and breeding success suggests that temporal or feeding constraints may be less important for Malaysian Plovers than for many holarctic shorebirds (Lank *et al.* 1985, Sandercock *et al.* 1999).

Malaysian Plovers re-nested many times in a season and intervals between clutches were shorter than those reported for many other plovers (Warriner *et al.* 1986, Fraga & Amat 1996, Amat *et al.* 1999b). For long-lived taxa such as shorebirds, costs to survivorship or future breeding potential

could limit the number of breeding attempts in a single year (Verhulst & Tinbergen 1991, Nilsson & Svensson 1996, Amat *et al.* 1999b). Female Malaysian Plovers may be able to obtain sufficient energy reserves to quickly re-nest because, compared to most holarctic shorebirds, they may have better initial body condition. This may be due to the lack of migration, the near optimal thermoregulatory environment during the winter and spring months, and access to abundant and reliable food supplies (Hegyí & Sasvári 1998). Throughout our entire study area there were wide mudflats with high *Scopimera* crabs densities immediately adjacent to Malaysian Plover nesting habitat ($n = 270$ quadrates, 108 ± 7.3 *Scopimera* burrows m^{-2} ; Yasué 2006). There also may be lower survivorship costs to Malaysian Plovers breeding late in the season compared to arctic species (Nilsson & Svensson 1996) because they do not undergo energetically costly migration shortly after breeding (Myers 1981). These results support previous work demonstrating that migratory populations of Kentish Plovers tend to have shorter breeding seasons and single broods, whereas mixed resident and migrant populations frequently have successive clutches (Boyd 1972, Warriner *et al.* 1986).

Although both parents contributed to parental care throughout the entire fledging period, Malaysian Plovers may still incur relatively low total parental care costs due to the favourable climate. When we conducted incubation observation in 2004 and 2005, mean temperatures and cloud cover were $33 \pm 0.12^{\circ}C$ and $45 \pm 1.6\%$, respectively. On 60% of the sampling periods, cloud cover exceeded 50% while on 91% of the sampling periods, temperatures ranged from 30 – $38^{\circ}C$. This is close to the optimum shorebird incubation temperature of 36 – $38^{\circ}C$ (Webb 1987). Consequently, on sampling periods in which there was high cloud cover, nests were frequently observed unattended for the entire 1–2 hour sampling period (10% of observations). This occurred more often in the late afternoon in June and July as temperatures dropped and the rainy season began. During the day, nests were attended by one of the adults for only 69% of the time (Yasué & Dearden 2008b),

leaving ample time for adults to meet daily feeding requirements, gain energy reserves for future clutches, or even care for a chick. Low nest attendance has also been documented in Hooded Plovers in warm climates in southern Australia (Weston 2000). In holarctic environments, birds have higher incubation times and spend more time brooding young chicks because of colder temperatures (Norton 1972, Martin 1987, Visser & Ricklefs 1993). For example, Dunlin *C. alpina* and Baird's Sandpipers *C. bairdii* in Alaska had 24-hour incubation periods of 97–98%, while diurnal nest attendance for Northern Lapwings *Vanellus vanellus* in Norway and Snowy Plovers in the United States was 89% and generally exceeded 80%, respectively (Norton 1972, Purdue 1976, Larsen *et al.* 2003).

Parents may also expend relatively little energy searching for safe and profitable feeding areas for chicks. At our field sites, Malaysian Plover chicks fed on mudflats and beaches as well as wetlands or shrubby vegetation behind the beaches. Thus they could move and continue to feed in a different part of their territory if they were disturbed by people, conspecifics, or predators. Moreover, the open structure of the beach allowed those parents that were feeding on the mudflat to simultaneously watch chicks and defend territories from conspecifics.

The reduced time required to thermoregulate young may have also contributed to the occurrence of brood overlap in Malaysian Plovers. Although there have been records of brood overlap, complete biparental care, and no parental role division in New Zealand Dotterels *Charadrius obscurus aquilonius*, Hooded Plovers in Australia, and Ringed Plovers *Charadrius hiaticula* in Germany, (Dowding *et al.* 1999, Weston 2000, Blomqvist *et al.* 2001), our study is one of the first to demonstrate this behaviour in a significant number of pairs (nine different pairs between the years). Moreover, two pairs simultaneously incubated two clutches and one pair managed to successfully hatch both clutches. As far as we know, this behaviour has not been documented in any other socially monogamous shorebirds.

A previous study suggested that biparental care and high mate and site fidelity between clutches may be due to the greater time required, or inability, of plovers to secure new mates or territories (Amat *et al.* 1999a). Intense competition for mates or space may lead to difficulties securing breeding territories part way through the breeding season (Ens *et al.* 1992). By remaining paired throughout the breeding season, Malaysian Plovers have multiple opportunities to lay successive clutches after nests fail or chicks fledge in high quality breeding territories.

Malaysian Plovers exhibited strong territoriality by defending habitats several months prior to, and during, the entire breeding season. Intense territoriality or limited high quality habitats could have led to high rates of mate or site fidelity, double-brooding or, biparental care (Haig 1987, Haig & Oring 1988, Lloyd 2008). Lloyd (2008) suggested that there may be higher adult survivorship, more complete parental care, and greater mate and site fidelity in south temperate or tropical *Charadrius* species compared to north temperate species. From our study it is unclear whether high territoriality was a natural tendency relating to year-round occupancy in an area by a shorebird. It is also possible that the recent rapid losses in beach breeding habitat as a result of development may have contributed to high site fidelity. Malaysian Plovers at our study site retained breeding habitats even when the quality of the habitat was reduced part way through the breeding season (Yasué & Dearden 2006b). Given the tremendous variability in breeding strategies within plover species (Johnson *et al.* 2006, Székely *et al.* 2006), to assess the generality of our results, research is needed to measure site or mate fidelity in different Malaysian Plover populations where there is much greater breeding habitat availability.

Almost half of the population laid successive clutches and half of the breeding attempts successfully fledged chicks. Thus for many pairs, successive clutching was an important strategy for plovers to fledge at least one clutch in the season. Successive clutching may be an adaptive strategy for long-lived species that live in environments

with substantial intra- and inter-year variability in breeding success (Page *et al.* 1983, Wallander & Andersson 2003). During good breeding years, birds can attain very high annual fecundity while incurring low costs to body condition to buffer years with low productivity (Strauss & Dane 1989, Oring *et al.* 1993, Wallander & Andersson 2003). In our study, hatch success was much greater in 2004 than in 2005. The low hatch success between April to early June due to high predation rates and construction activities (Yasué & Dearden 2006b) may have contributed to differences in how lay date and failure date affected the likelihood of re-nesting between the two years.

Despite the apparent lack of seasonal decline in breeding success, birds were less likely to lay successive clutches if they bred later on in the season. One explanation for this result is that older individuals or higher quality individuals may be able to establish territories earlier in the breeding season, and also may be more likely to lay successive clutches (Holmes *et al.* 1992, Forslund & Pärt 1995). Alternatively, there could be seasonal changes in factors other than prey availability, such as maximum tide heights (Tulp 1998) or predation. These factors could also reduce the success of nests later in the breeding season and thus limit the potential benefits of successive clutching. We did not monitor nests until the end of the breeding season so it is possible that we may have detected a seasonal decline in breeding success if we had monitored nests in August and September. Unusually high tides enhance flood risk for Malaysian Plovers and flooding was a significant cause of clutch failure at our study site (Yasué & Dearden 2006b). Although maximum tide heights are high in January and February and could affect the start of the breeding season, tide heights were low throughout the summer and into the fall. For this reason, it is unlikely that tides influenced the end of the breeding season.

Most studies on avian breeding strategies have been conducted in north temperate environments which include less than one quarter of the global bird species (Martin 2004, Moreno 2004). Our results suggest that many of the conditions

characteristic of a tropical breeding environment could have contributed to the short intervals between clutches, successive monogamy, high within-season site fidelity, double-brooding, and complete biparental in the Malaysian Plover. There are very few tropical shorebird studies with which to compare our results. This makes it difficult to identify possible patterns in breeding behaviour that are caused by differences in temperate and tropical conditions (Tyler 1978, Cramp & Simmons 1983, Lloyd 2008). Ecological and evolutionary research aimed at identifying the factors shaping parental care or mating strategies is hindered by the lack of data in tropical environments (Reynolds & Székely 1997, Thomas *et al.* 2003). It is possible that biparental monogamous successive clutching and other *unusual* breeding strategies may simply be under-documented, due to the paucity of shorebird research in tropical environments. More research on tropical species is needed to identify the social, ecological or physical parameters constraining breeding strategies and also determine the full extent of variability in shorebird breeding behaviour.

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SAMENVATTING

De leefomstandigheden van tropische steltlopers wijken in veel opzichten af van die van hun verwanten in arctische en gematigde streken. Zowel temperatuur als voedselaanbod zijn veel constanter in de tropen dan op hogere breedtegraden. Wat dit voor gevolgen heeft op het broedgedrag van tropische steltlopers is onvoldoende bekend. In dit onderzoek werd het broedgedrag van de Maleise Plevier *Charadrius peronii* bestudeerd. Gedurende twee broedseizoenen (november tot juli) werden de nestpogingen van 54 en 79 gekleurde plevieren gevolgd op 15 stranden aan de Golf van Thailand. In beide jaren begon bijna de helft van de paren aan een tweede legsel. Dit betrof vooral paren waarvan het eerste legsel verloren was gegaan. Elf paren begonnen aan een tweede legsel terwijl de jongen van het vorige legsel nog niet onafhankelijk waren. In de meeste gevallen werd het tweede legsel met dezelfde partner in hetzelfde territorium geproduceerd als het eerste. Slechts vijf vogels (van 52) begonnen een tweede legsel met een nieuwe partner, waarschijnlijk omdat hun vorige partner was overleden. Mannetjes en vrouwtjes deelden de ouderzorg, ook als het bebroeden van het tweede nest overlapte met de zorg voor de jongen van het eerste nest. Er waren geen verschillen in legselgrootte en afmetingen van de eieren tussen eerste en tweede legsels. In beide jaren was de kans dat er aan een tweede legsel begonnen werd afhankelijk van de datum waarop het eerste legsel verloren ging; vogels die hun nest laat in het seizoen verloren begonnen zelden aan een tweede legsel. In 2004 speelde bovendien de datum van het begin van het eerste legsel mee bij de beslissing een tweede nest te beginnen. Het voedselaanbod (in de vorm van krabben) in het territorium had geen invloed op de kans op een tweede legsel. Deze gegevens suggereren dat de duur van het seizoen en het voedselaanbod weinig beperkingen opleggen aan de broedstrategie van deze tropische steltloper. Daardoor zijn tweede en derde legsels voor deze soort normaler dan voor de meeste verwante soorten op hogere breedtegraden. (KK)

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