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Providing parental care entails variable mating opportunity costs for male Temminck's stints

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Abstract Males of many species theoretically face a fitness tradeoff between mating and parental effort, but quantification of this is rare. We estimated the magnitude of the mating opportunity cost paid by incubating male Temminck's stints (*Calidris temminckii*), taking advantage of uniparental care provided by both sexes in this species. "Incubating males" provide all care for an early clutch, limiting subsequent mating possibilities. "Non-incubating" males include males that failed to obtain, lost to predation, or actively avoided incubating clutches. These males were free to pursue extrapair copulations and to mate with females laying later clutches, which females usually incubate themselves. Male incubation classes did not differ in measures of quality, and many individuals changed classes between years, suggesting the use of conditional reproductive tactics. However, specialist non-incubators may also exist. Using microsatellites to assign parentage, we compare males' total fertilizations and the subset "free of care" fertilizations between incubation classes. Incubators were more likely to gain at least one fertilization per season and averaged one more per season than non-incubators. However, successful non-incubators were more likely to gain "free of care" fertilizations, averaging two more than successful incubators. The relative success of male incubation classes also changed with local sex ratios. With higher female proportions, non-incubators gained disproportionately more offspring, suggesting that the use of tactics should be partly determined by the availability of potentially incubating females. Overall, we estimate the opportunity cost of incubating to be 13–25 % of the potential annual reproductive output.

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Introduction

Providing parental care usually entails a cost to subsequent reproductive efforts or survivorship (Williams 1966; Low 1978; Magrath and Komdeur 2003). Quantifying the ecological and evolutionary cost of parental care remains a central question and controversy in evolutionary ecology (Lessells 2006; Parker 2006; Harrison et al. 2009). From a long-term perspective, providing parental care is assumed to carry with it a survival cost and in the short term to reduce opportunities for additional matings or breeding effort (Low 1978; Whittingham and Dunn 2001). This latter tradeoff is stronger in species where parental effort is available to a limited number of brood members and/or shareable among them (Lazarus and Inglis 1986) and less strong if parental effort is not

shareable within broods that may even include ova from multiple females (e.g., Wisenden 1999).

To date, the tradeoff between parental and mating effort has been largely assumed. For male birds, negative associations between measures of paternal care and effort to gain extra copulations provide indirect evidence of the tradeoff's importance (Magrath and Komdeur 2003). However, because the tradeoff generally stems from temporal or energetic limitations, high-quality phenotypes may be able to invest more in both care and mating, resulting in positive associations in some observational studies (Qvarnström 1997; Johnsen et al. 1998). Factors such as the value of the brood (Székely and Cuthill 2000); the availability of limited resources (Smith 1995); the social environment, i.e., sex ratios (Magrath and Elgar 1997); and the behavior of other individuals (Stiver and Alonso 2009) also affect allocation decisions. But extrapair offspring are a common phenomenon in avian breeding systems and can form a significant component of individual male fitness (Griffith et al. 2002; Westneat and Stewart 2003). Therefore, quantifying the potential fitness (e.g., fertilizations) that could be accrued in the absence of parental care will provide insight into the evolution of mating systems and alternative reproductive tactics in animals. Obtaining such direct measures of this opportunity cost is usually difficult.

The wide range of breeding systems found in shorebirds have made the group fruitful for understanding mating effort and parental care tradeoffs (Székely et al. 2007; Thomas et al. 2007; Olson et al. 2009). Our study exploits one such system to analyze these opportunity costs and benefits. Temminck's stints (Calidris temminckii) have a "serial polygamous" system (Pitelka et al. 1974) in which either a male or female provides exclusive care for a clutch (Hildén 1975). Biparental care at a single nest has never been documented. Males of this small predominantly sub-arctic-breeding wader display on small territories and actively pursue females. If mating occurs, the pair bond is brief, lasting only the time for a female to complete a clutch, typically of four eggs. As is currently understood and presented in the literature, females lay this clutch in the male's territory and the male typically incubates it, but often not immediately. Males may delay the onset of incubation; some clutches go unincubated for up to a week (Kokhanov 1973; Hildén 1979). Most males continue displaying and attempt to attract a new female to their territory. Once they start to incubate, males leave eggs to forage and only rarely leave to display. Males that lose clutches to depredation early in the breeding season resume display and territory defense (Hildén 1979). However, some nests remain unincubated by either sex, apparently due to sexual conflict over parental responsibility (Hildén 1975; Emlen and Oring 1977; this study). Males may abandon these nests to invest more in mating effort, becoming "extrapair" mates or mating with females who will assume incubation responsibilities for a clutch. Parental and mating efforts are thus largely mutually exclusive activities for male Temminck's stints.

After completing her first clutch, a female typically leaves the male's territory and remates with another male on his territory, where a second clutch is laid (Hildén 1979; Breiehagen 1989). This raises the possibility of a female's first male obtaining young in her second nest by carryover of sperm (e.g., Oring et al. 1992; Schamel et al. 2004). Females usually incubate these second clutches, but rarely they obtain incubation from a second male and lay a third clutch (observed once in our population, also Hildén 1975; Pienkowski and Greenwood 1979; Breiehagen 1989). Consequently, female-incubated nests are phenologically later in the season (Hildén 1965); in our population, male-incubated nests are initiated on average 6 days prior to females' (V-MP and KK, unpublished data).

To summarize, in the Temminck's stint breeding system, both sexes have the potential to provide parental care, mate multiple times, and obtain parental care from one or more partners. Females regularly lay two clutches with two males, while males can father offspring that are cared for by females or, through extrapair copulation or sperm carryover, by other males. Incubation by either sex raises the possibility of sexual conflict over parental responsibility.

Taking advantage of this breeding system, we compare the additional mating rates of incubating males, which bear the costs of parental care, versus non-incubating males that do not. We use a measure that quantifies an end product that directly affects fitness and reflects the success of the mating effort: actual fertilizations and hatchlings fathered, as assessed by molecular parentage analyses. Incubating males are those found attending clutches or hatched broods. Non-incubating males include (1) those losing nests to predators, floods, or other factors during egg laying or prior to discovery during incubation (e.g., Rönkä et al. 2006) that do not obtain replacement clutches, (2) males failing to be chosen by females as potential incubators of clutches, and (3) theoretically, any males that invest solely in mating effort and actively avoid incubation.

Interpreting our results as measurements of opportunity costs depends somewhat on the extent to which males in each group are of comparable intrinsic quality, or arise due to chance events, versus differing in ways that would bias samples toward more or less successful males. Thus, we first test whether the two groups differ in a suite of phenotypic traits measuring aspects of quality. Many birds we classify as non-incubators occur due to destruction of their nests due to flooding, predation, and trampling. Half of nests were attempted to be protected from predation (see Methods), increasing the likelihood that nest loss was random relative to male incubation status. We also assess the likelihood of individuals changing categories from year to year and the direction of such changes. Finally, we examine behavioral data for

evidence of males that forego incubation (parental effort) and concentrate on mating effort.

To quantify the relative fertilization success between males providing and not providing parental care, we compare the success of incubators and non-incubators in terms of gaining "free of care" fertilizations, defined as genetically fathered eggs that are incubated and raised either by a female or by another male stint. To put these numbers in perspective, we also compare the total number of fertilizations, including self-incubated eggs for incubators, for the two classes of males. Lastly, we investigate if a social population factor, the local sex ratio (Emlen and Oring 1977), influences the relative success of males pursuing each tactic (Alonso 2009).

Methods

Study area

The study area is situated in the northern Baltic Sea on the Finnish coast of the Bothnian Bay south and east of Oulu (centered ca. 65° N, 25°30′ E, extending about 30 km north to south and 50 km west to east, Fig. 1). The Bothnian Bay Temminck's stint population, currently ca. 160 territories, is separated by a few hundred kilometers from the main breeding range in Fennoscandia (Rönkä et al. 2006; Koivula et al. 2008; Sundström and Olsson 2009). This population is declining (Rönkä 1996; Koivula et al. 2008), and we studied birds at five main remnant sites that included one to ca. 15 territories per year (Fig. 1). There were no confirmed territories of the species breeding between these distinct breeding localities.

Breeding data and DNA sample collection

Breeding Temminck's stint adults were captured and their breeding attempts monitored closely between 1994 and 2011. Intensive searching for territories and nests started in the middle of May and continued throughout the breeding season. Prospective hatching dates were approximated based on the number of eggs found during laying or, for nests found during incubation, by floating an egg or two in water (Westerskov 1950; Liebezeit et al. 2007). Nests were checked every 1–5 days until hatching. Adults were caught with mist-nets set over the nest during incubation, or above newly hatched chicks, and were marked with individual combinations of color rings and a numbered steel ring. Individuals seen in the study site were meticulously recorded. Incubating a replacement clutch was rare; our data included only two cases of males incubating a second clutch within a season following the loss of their first, and only four cases in 16 years of nesting data have been confirmed. These nests produced no offspring samples.

Collection of blood samples from adults and young was initiated in 2001. Blood was sampled from the brachial vein in adults. Between 2003 and 2006, chicks were ringed with a numbered metal ring and blood was sampled from the tarsal vein. Chicks found dead and all unhatched eggs were collected for DNA extraction.

To obtain direct information on individual male breeding tactics, detailed behavioral observations were made by an observer (KK) in 2012 at the last remaining small breeding sub-population from this study, Siikajoki (64° 50′ N, 24° 35′ E). Other sites were extinct or limited to single displaying individuals. Observations focused on behavior of males as incubators or non-incubators throughout displaying, mating, and incubation periods. All nests were located, but no capture or blood sampling was performed.

DNA extraction, microsatellite amplification, and sexing

DNA was extracted from blood and other tissues by using the UltraClean Blood Spin kit (MoBio) according to the instructions of the manufacturer. DNA contamination was suspected in three samples that were discarded from the analyses. Nine microsatellite loci originally designed for dunlin (*Calidris alpina*: Calp2; Wennerberg and Bensch 2001), ruff (*Philomachus pugnax*: Ruff5, Ruff6, Ruff8, and Ruff10; Thuman et al. 2002), barn swallow (*Hirundo rustica*: Hru2; Primmer et al. 1995), oystercatcher (*Haematopus ostralegus*: 49F6; van Treuren et al. 1999, red knot *Calidris canutus*: Pgt83; GenBank accession number AY198173), and great snipe *Gallinago media*: Gme3 (Saether et al. 2007) were amplified.

Laboratory analyses were done in the US Geological Survey, Alaska Science Center lab in Anchorage, Alaska (samples from 2003 to 2005) and in Oulu (samples from 2004 to 2006). In Oulu, the PCR amplifications were performed in 10 μl reaction volumes. The reactions contained 50–250 ng of template DNA, 1.0 μM of each primer, 0.1 mM of each dNTP, 1 μl of 10× PCR buffer, 2–2.5 mM of $MgCl_2$, and 0.1 μl of DNA polymerase (Dynazyme or Biotools DNA-polymerase). The amplification profile was 94 °C for 1 min followed by 35 cycles of 94 °C for 30 s and then either 50 °C for 49F6 or 58 °C for Calp2 for 30 s for annealing and 72 °C for 45 s for synthesis. A touch-down profile with annealing temperatures from 58 to 54 °C for Calp2; 50 to 46 °C for Ruff5, Ruff6, Ruff8, Ruff10, Pgt83, and Gme3; and from 53 to 47 °C for Hru2 was used. The PCR ended with final extension in 72 °C for 10 min. The reactions were run with ABI 3730, and loci were scored with GeneMapper v.3.7.

Lab work done in Anchorage followed protocols outlined in Mulard et al. (2009). A LI-COR 4200 LR automated sequencer, using Base ImagIR (LI-COR, Inc., Lincoln, NE, USA) was used to separate alleles. Samples from both laboratories were calibrated by assigning the allele sizes of the

Fig. 1 Location of the study populations at the Bothnian Bay, Finland. Modified from Pakanen (2011)
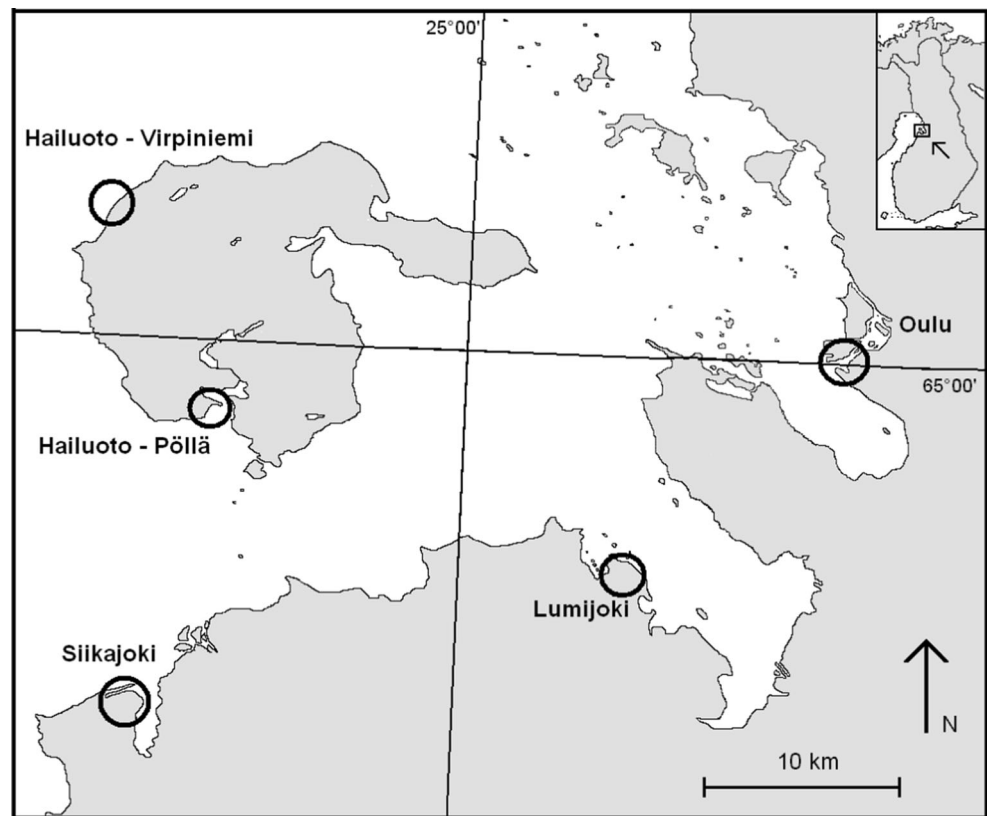
Alaskan laboratory to the sizes obtained in Oulu, by repeating the runs in both labs from 15 to 86 samples per locus. All samples were sexed using the PCR conditions described in Griffiths et al. (1998), except that we used a touch-down for annealing temperatures from 48 to 44 °C. If PCR amplifications of this locus were not successful (five individuals), birds were sexed based on heterozygosity of any hemizygous microsatellites located on the Z-chromosome (Ruff5, Ruff6, and Ruff10; Thuman et al. 2002; Rönkä et al. 2008) and by behavioral cues, for example, male display.

Descriptive genetic analyses

The microsatellite results were first tested for null alleles, allele dropouts, and scoring errors with Microchecker v 2.23 (von Oosterhout et al. 2004). Allele frequencies were tested for Hardy–Weinberg equilibrium in both sexes, also separately for males (using all the loci) and females (excluding the sex-linked loci). Linkage disequilibrium across loci was checked with program Genepop v. 3.4 (Raymond and Rousset 1995). See Appendix A for further details.

Parentage analysis

Parentage analyses were performed with CERVUS 3.03 (Marshall et al. 1998). The program first calculates allele frequencies from individual genotypes and then simulates to estimate the resolving power of the loci given their allele frequencies. In addition, it estimates critical values for log-likelihood statistics (LOD scores) and Delta (difference in LOD scores between the most likely and second most likely candidate parent), so that parentage assignments can be evaluated for given levels of confidence. A positive LOD score indicates that a male/female is more likely to be the father/mother of an offspring than is an individual randomly drawn from the population. Once LOD scores are calculated for all individuals, the male/female with highest score was assigned as the putative parent. See Appendix B for further details.

Males of the study population

Males that were confirmed to have been present in the study area during the mating and laying periods were included in the analyses each year. These included males seen, plus three males that were not seen, but identified as fathers in genetic parentage analysis. Finding only three males not visually encountered shows that visual coverage was almost entirely comprehensive and suggests that few additional males were both not visually confirmed and did not father young. The data consists of 122 male-years from 59 different males; 37 males were present in two or more years. A male-year is therefore a single breeding season of a particular male individual.

Individual quality and consistency of incubation behavior

We investigated whether incubators and non-incubators were similar in quality, using three potential measures. For age ($n=$ 122), we used years since color ringing to avoid bias between local recruits and immigrants, since the latter cannot be aged by year of birth. Age was analyzed with a generalized linear mixed model (PROC GLIMMIX) with a Poisson distribution and log link. The second measure was status as a local recruit or immigrant ($n=122$), which differ in measures of local reproductive success (Pakanen et al. 2010, 2011). The third measure was fertilization success the previous year (yes versus no, only 2004–2006, $n=60$). Immigration and prior success were analyzed with a binary distribution, including individual identity as a random effect, with degrees of freedom calculated using the Kenward–Roger method.

Twenty-four (65 %) of the 37 males present in two or more years had different incubation statuses between years. To investigate the consistency of individual incubation status, we used a method developed by Pogány et al. (2008). First, we calculated the absolute difference between all possible comparisons of incubation status. For example, a male breeding in three seasons (a, b, c) had all possible differences between incubation status calculated as |a–b|, |a–c|, |b–c|. For each individual, the proportion (p) of identical decisions between seasons was calculated as the number of season pairs with identical strategies/the number of all possible comparisons. The mean of these proportions for all individuals was the test statistic (ΔX_{crit}). We then used a resampling approach (resampling stats for Excel), in which each observation was shuffled into a new position without replacement and the mean of the proportions calculated as above (ΔX). Shuffling was iterated 10^4 times, and the number of iterations producing ΔX larger than ΔX_{crit} was calculated as the P value.

Incubation status and measures of mating success

A male's "Incubation status" each year was our primary analysis variable. "Incubators" were males captured on or observed attending nests that year. "Non-incubators" were males confirmed present, but not found incubating a nest. Two males first found displaying late in the breeding season, one each in 2004 and 2005, were not included due to their absence during mating and laying periods; these transient males fathered no young and were not encountered in later years.

Annual male fertilization success was the sampling unit. Fertilizations included all genetically fathered chicks (hatchlings) plus unhatched eggs from which DNA was successfully extracted. Including all genotyped "offspring," whether they survived or not, provided our most robust summary of males' mating success. Many eggs were lost prior to hatching, due to nest predation, flooding, trampling, and

human disturbance, but we extracted DNA from some of these. We regard these losses as primarily due to chance events and assume that those sampled were a random subset of fertilizations that occurred in the population. The nature of nest losses supports this. Predation is partly from introduced predators or human pets (authors' observations), freak weather events causing high water levels, trampling by livestock, and human disturbance at breeding sites. As an example of human disturbance, nine failed nests that were disturbed by illegal midsummer beach parties on Siikajoki in 2004; we suspect that by the time the birds returned to incubate these nests, the embryos had died. DNA was extracted from five nests, but even within these nests the extraction failed with some eggs. Furthermore, as a conservation measure for this threatened population, half of the nests were protected from predation using protective cages placed over nests as they were found, in stages ranging from egg laying through incubation (Pauliny et al. 2008). Protecting a random sample of nests and the chance nature of disturbance increased the likelihood that our DNA samples represent a random subset of fertilizations.

We calculated the "total fertilizations" obtained by each male, which included all genetically fathered chicks and eggs. To estimate the opportunity cost of incubation, we calculated the number of "free of care fertilizations," defined as eggs that were incubated by another male or female. We refer to these as "free fertilizations," reflecting the absence of paternal care costs, although mating effort costs in terms of male displaying, female pursuit and territorial defense remain. As a more downstream measure of fitness, but with fewer data, we also calculated for each male the number of fathered hatchlings and free of care hatchlings, excluding unhatched eggs, which are subsets of fertilization success.

For each male in each year of this study, our dataset included: (i) age (years since being color marked), (ii) incubation status, (iii) total number of fertilizations, (iv) number of "free of care" fertilizations, (v) number of hatchlings, and (vi) number of free of care hatchlings fathered. Small annual sample sizes excluded the possibility of analyzing years separately, and data were pooled across years. Our data consisted of 73 incubating and 49 non-incubating male-years (Table 1).

Many males annually fathered no chicks or unhatched eggs that were sampled, in part due to the nests lost to predation. This included both incubators ($n=20$, 27 % of incubator male-years) and non-incubators ($n=23$, 47 % of non-incubator male-years). Because of the large number of zeros, we analyzed two measures of male success. First, we tested the relationship between incubation status and the probability of a male gaining at least one "free of care" fertilization or at least one fertilization overall (generalized linear mixed model (PROC GLIMMIX, binomial distribution with logit link, and Kenward–Roger method)). Incubation status was entered as the main explanatory variable, with individual identity and

Table 1 Yearly and overall mean fertilizations (±SE) and free fertilizations gained by incubating and non-incubating males in the study population

	Incubating male-years		Non-incubating male-years	
	Mean fertilizations	Range	Mean fertilizations	Range
2003	*n*=14 (9 successful)		*n*=11 (9 successful)	
Fertilizations	2.1 (±0.53)	0–6		
Free fertilizations	0.6 (±0.27)	0–3	2.9 (±0.83)	0–9
2004	*n*=16 (10 successful)		*n*=10 (4 successful)	
Fertilizations	2.3 (±0.60)	0–7		
Free fertilizations	0.6 (±0.29)	0–4	0.7 (±0.33)	0–3
2005	*n*=23 (19 successful)		*n*=12 (8 successful)	
Fertilizations	2.7 (±0.43)	0–9		
Free fertilizations	0.2 (±0.22)	0–5	1.4 (±0.40)	0–4
2006	*n*=20 (15 successful)		*n*=16 (5 successful)	
Fertilizations	2.6 (±0.46)	0–7		
Free fertilizations	0.6 (±0.23)	0–4	0.6 (±0.27)	0–3
2003–2006	*n*=73 (53 successful)		*n*=49 (26 successful)	
Fertilizations	2.5 (±0.25)	0–9		
Free fertilizations	0.5 (±0.12)	0–5	1.3 (±0.26)	0–9

N number of male-years, *Successful* number of males obtaining at least one fertilization

the annual site entered as random factors to account for unknown effects of the individual and site-specific effects. We repeated the above analyses for hatchlings only. Second, we repeated these analyses using total "free of care" or total fertilization success (number of fertilizations, including 0 s), or based on hatchlings, using a similar approach with a Poisson distribution, log link, and Kenward–Roger method.

Parallel logic about parental care–reproductive effort tradeoffs applies to female Temminck's stints, but our analyses are limited to males for two technical reasons. Since females have lower nest site fidelity, within and between years, our capture, sampling, and resighting data are less complete (see Pakanen et al. 2010 for details). Secondly, since three of our nine microsatellite parentage markers were hemizygous and thus scored only for males, maternity assignments were less reliable, particularly between mothers and daughters.

Local sex ratios

To quantify the effects of the local social environment on the relative success of each strategy, we computed local adult sex ratios for each site and year, as a proxy for seasonal operational sex ratios (Emlen and Oring 1977). We assume that within-season variation in sex ratios, and its influence on fertilization success, was minimal in our study. The short northern breeding season and the especially short and synchronized initiation of nesting in our Temminck's stint

population suggest that a single summed seasonal sex ratio is a robust estimate (see "Basic population results").

Sex ratio estimates of the smallest site populations may be due to chance and biased (Donald 2011); therefore, we removed data from the island of Hailuoto for this analysis (two annual sites). This population contained two spatially separated sites (see Fig. 1), and these sites contained small numbers of individuals (<10 total individuals each). In addition, one non-incubating male (one male-year) was excluded, as it was found displaying alone on a site and no sex ratio values could be calculated for that annual site. This step excluded nine males in total and leaves 113 male-years contributing toward this analysis. Including these sites in analyses produced the same qualitative results. Individual identity and annual site were entered as random effects in the model to account for non-independence of males in the same site and of the same males in different "male-years."

Sex ratio was calculated as: number of males/total adult individuals for the annual sites. Our data includes values for 10 annual sites; two remnant sites contained birds each of the 4 years of study, but one site contained birds only in two of the 4 years. For the local sex ratio calculation, male numbers included all 113 male-years with complete data (occurring on the included sites), plus six additional male-years uniquely reconstructed from offspring genotypes without identified fathers. Similarly, female numbers included individual sightings and DNA confirmations, plus 25 unique individuals reconstructed from offspring genotypes sampled from male incubated nests. Reconstructed female individuals contributed

substantially more than males, reflecting their greater mobility and the smaller number that were color-ringed (see above).

We used SAS statistical software (version 9.1; SAS Institute, Cary, NC, USA) for all analyses unless stated otherwise. Means are presented with standard errors or 95 % confidence limits.

Results

Molecular results

Possible null alleles were detected in Calp2 and Ruff5 for males, but not in females. In the male population, these loci showed a lack of heterozygotes also in the HW test (see Appendix A). Linkage disequilibrium was not detected.

Basic population results

Between 2003 and 2006, 153 nests were found (nine at the brood stage) including 75 incubated by males (including two replacement nests) and 50 by females. Incubators were not identified at 28 nests, all of which were destroyed early during the breeding phase. Sixty-three nests (41 %) were destroyed before sampling took place. We protected 77 of the 153 nests, of which 17 (22 %) were predated. Of the 76 nests not protected, 34 (45 %) were predated. Unsampled nests included 35 nests with the incubator identified, 23 male- and 12 female-incubated nests.

DNA was scored for 265 offspring from 90 nests (mean 2.9/brood; 195 from chicks and 70 from unhatched egg embryos). Unsuccessful DNA extraction or scoring occurred for an additional 48 samples, including 45 unhatched eggs and three contaminated samples. Twenty nests (22 %) contained fertilizations by two or more males (multiple paternity). Of 52 male-incubated nests sampled, 10 (19 %) included fertilizations by other males. Fathers could not be confirmed for 18 of the 265 (7 %) scored samples from eight different nests and were not included in analyses. Of these, 16 samples were from female- and two from male-incubated nests. No cases of females laying in other female's nests were documented.

Incubating males obtained 181 fertilizations during 73 male-years. Incubators cared for 145 of their own eggs and obtained 36 additional free of care fertilizations, including 32 in female-incubated nests and four in nests incubated by other males. Sixteen incubators gained "free of care" fertilizations in female-incubated nests. For 13 of these 16, maternal samples from own nest were available for comparison with maternal DNA from their "free of care" fertilizations. Three of these 13 involved the same female for both nests, even though these females' nests were not in the first males' territories. This suggests that sperm storage and/or persistent pair bonds account for about 23 % of incubators' free fertilizations. Non-

incubating males obtained 66 fertilizations during 49 male-years, 58 in female-incubated and eight in male-incubated nests. Table 1 summarizes the number of males of each status obtaining at least one fertilization per year (in male-years) and mean male free and total fertilization success over the 4-year study.

Individual quality and incubation strategy consistency

Incubation status did not differ for any of the potential measures of male quality analyzed (Table 2): male age (years since being color ringed; $n=122$, $F_{1, 120}=0.01$, $p=0.95$), immigrant status ($n=122$, $F_{1, 120}=0.90$, $p=0.34$), or male fertilization success in previous year ($n=60$, $F_{1, 58}=0.14$, $p=0.71$). Twenty-four of 37 males that were present in two or more years changed their incubation status between years. No individual consistency in incubation tactic was observed, and incubation status was random across years ($P=0.52$, $\Delta X_{crit}=0.49$). A male's reproductive tactic in 1 year was completely unrelated to his reproductive tactic in the following year.

Incubation status and local sex ratio effects

We estimated differences in fertilization performance of incubators and non-incubators while controlling for local sex ratio. Non-incubators were more likely than incubators to obtain at least one free fertilization (LS means probability: incubators= 0.23 [0.14–0.35] versus non-incubators=0.53 [0.37–0.69]; main effect of incubation status: $F_{1, 120}=9.94$, $p=0.002$) and had higher total free fertilization success (LS means: non-incubators 1.12 ± 0.22 versus incubators 0.37 ± 0.02; Table 3). In the raw data, non-incubators averaged about one free of care fertilization more than incubators (Table 1).

Incubation status also significantly explained male probability of obtaining at least one fertilization, but in contrast, incubators performed better than non-incubators (LS means probability: incubators=0.73 [0.58–0.84] versus non-

Table 2 Counts of male-year data for the three quality measures for each incubation status

	Incubation status	
	Incubator	Non-incubator
Age (years since color ringed)		
Mean (±SE)	2.1±0.29	2.3±0.33
Immigration status		
# of local recruits	53	29
# of immigrants	20	20
Previous fertilization success		
# successful	23	16
# unsuccessful	11	10

Table 3 Effects of male incubation status, local sex ratio from 10 annual sites (see "Methods"), and their interaction on free and total fertilizations

Independent variable	d.f.	Estimate±SE	F value	p value
Free of care fertilizations success				
Incubation status	1, 109	11.23±2.99	14.15	<0.001
Sex ratio	1, 109	4.70±3.64	2.30	0.13
Incubation status×sex ratio	1, 109	−17.06±4.98	11.75	<0.001
Total fertilizations success				
Incubation status	1, 109	5.66±1.97	8.23	0.005
Sex ratio	1, 109	−1.33±1.59	15.13	<0.001
Incubation status×sex ratio	1, 109	−10.73±3.38	10.08	0.002

Generalized linear mixed models (Poisson distribution, log-link) for male years (n=113) of (a) the number of free of care fertilizations and (b) the total number of fertilizations

Fig. 2 Linear regressions of the mean total fertilization success per site as a function of local sex ratio, for incubators (*solid dots* and *thick line*) and for non-incubators (*open dots* and *narrow line*). One annual site contained no non-incubators; therefore, one open data point could not be generated

incubators=0.53 [0.36–0.70]; main effect of incubation status: $F_{1, 120}$=3.99, p=0.048), and incubators obtained significantly more total fertilizations than non-incubators (LS means: non-incubators 1.17±0.19 versus incubators 2.28±0.24; Table 3). The raw data show about one fertilization more for incubators compared with non-incubators, on average (Table 1). Parallel analyses of hatchlings only, excluding identified eggs lost due to nest depredation or otherwise failing to hatch, produce similar patterns as those on all fertilizations, despite smaller sample sizes (Appendix C).

The general patterns of fertilization success differed as function of local site sex ratios, which were generally male biased (mean=0.59, range 0.50–0.67). Both free of care and total fertilization success were explained by incubation status, sex ratio explained total success, and the interactions between sex ratio and status were significant for both (Table 3). The interaction terms shows that site sex ratio differently influences the free and total fertilization success of incubating and non-incubating males. For visual purposes, we plot linear regressions at the site scale of mean individual total fertilizations for each incubation status against sex ratio (Fig. 2). Non-incubating males fertilized significantly more offspring at lower sex ratios (higher female proportion, β=−23.21±5.86, p=0.005), but sex ratio did not significantly explain incubator fertilizations (β=−1.08±4.33, p=0.81). Sex ratios in the study were equal or male-biased, and non-incubators may have exceeded the success of incubators at the lowest sex ratio values, with comparable success at mildly male-biased sex ratios. One annual site contained no non-incubating males; thus, no value could be generated for non-incubator fertilization success.

A case of early non-incubation?

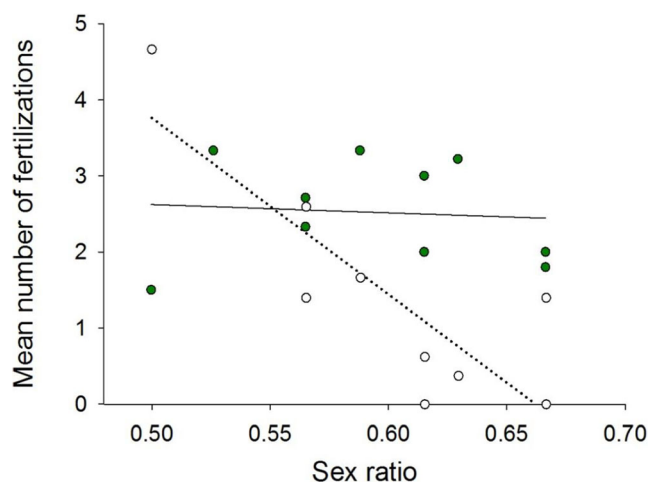Detailed observations at one site during 2012 identified 17 individuals, including 11 males and three females recognized by rings, and three unringed birds (two males and one female, based on behavior). The site sex ratio was thus more highly male-biased, 0.77, than during earlier years of the study. Only six clutches were laid, of which five were found during egg-laying and one during the brood phase. No nests were depredated, although one was destroyed by flooding after abandonment.

Of the 11 marked males seen displaying, seven were seen with a female and thus considered mated at some phase of the season. The six nests occurred on five territories. Two were incubated by males, two by females, and two received no incubation and were abandoned. One male was confirmed to be an active non-incubator. He displayed throughout the breeding season and was the only male displaying after 10th June. He paired with two females that laid clutches on his territory. The first female he paired with had already laid a clutch with another male. This female incubated the newly laid nest (her second) and stayed 3 weeks. The male continued active display in a new territory about 400 m from the first and mated with a second female, which laid a clutch and started incubation. In early July, after the mating season was over (latest initiated nest ever recorded in this population is 29 June), the male returned to his first mate, took responsibility for the nest several days before hatching, and cared for the chicks after hatching.

Discussion

The importance of a tradeoff between parental and mating effort has long been suggested (Williams 1966; Low 1978), but also cautioned against (Stiver and Alonso 2009). Our study estimates the minimum magnitude of the mating opportunity cost incurred by incubating male Temminck's stints, in

terms of its impact on annual potential reproductive success at different local sex ratios. We quantified the short-term cost of providing parental care in terms of lost potential fertilizations. Many studies quantifying this tradeoff in birds rely on behavioral or energetic proxies of effort (e.g., Westneat 1988; Smith 1995; Magrath and Elgar 1997; Pitcher and Stutchbury 2000; Magrath and Komdeur 2003). Our study measures a closer proxy for the relative evolutionary payoffs of this tradeoff in this system. Males that performed active care, i.e., incubators, gained significantly fewer free of care fertilizations than males that performed no parental care, i.e., non-incubators. The actual cost was about two free fertilizations lost per successful incubator compared to a successful non-incubator. The corresponding value including unsuccessful individuals is about one fertilization. These effect sizes represent a large proportion of annual reproductive success in this species with a clutch size of four eggs. Under the classical model of the Temminck's stint mating system (Hildén 1975), each individual is parent to eight eggs. Thus, differences of one to two fertilizations represent substantial fractions, e.g., 0.13–0.25, of a male's potential annual fertilization success. There is no reason to believe this difference would not carry through to a similar difference in hatching and survivorship of young. Finally, the magnitude of this advantage changed with the local sex ratio. Non-incubating males gained relatively more fertilizations when females were more available, while incubator success remained unchanged (Fig. 2).

Our data suggest substantial incompatibility between providing parental care and mating effort. Fifty-three percent of non-incubators obtained at least one free fertilization, compared with 23 % of incubators. A small proportion of eggs in female incubated nests were fertilized by her first mate; thus, sperm storage from one clutch to the next may be a source of free of care young for incubating males in this and similar systems (c.f. Oring et al. 1992; Schamel et al. 2004). But obtaining such young is more than offset by the possibility of obtaining incubation for a complete additional clutch. Males often delay the onset of incubation apparently to invest in mating opportunities (Kokhanov 1973; Hildén 1975), providing prima facie evidence for this tradeoff between parental and mating effort.

Despite the opportunity cost estimated above, incubators obtained more annual fertilizations than non-incubators. Incubating males in polyandrous species in general have several behavioral options to obtain additional fertilizations, including strategic copulation to promote sperm storage (Oring et al. 1992; Schamel et al. 2004), timing mating with sexually active females (Emlen et al. 1998), and avoiding mating with previously mated females (Whitfield 1990). In some species, a parent exhibits brood desertion late in incubation or post-hatching (Székely et al. 1999; Szentirmai et al. 2007; Pierce et al. 2010), but the brief Temminck's stint pair bonds preclude this tactic. In our population, incubators were twice as likely

as non-incubators to obtain fertilizations during a season (Table 1). Among successful individuals, incubating males averaged one fertilization more than non-incubators, and incubators obtained 1.2 more when all individuals were considered. Providing sole parental care for young as in the Temminck's stint breeding system may be associated with higher long-term survival costs; our study did not quantify this component of the cost–benefit analysis. Nevertheless, some measurable costs do exist. One in five male incubators invested in the care of other male's fertilizations: a "hidden" cost of parental care (Møller and Birkhead 1993). By definition non-incubators cannot suffer this cost.

Our interpretation of these results as a measurement of an incubating male's mating opportunity cost assumes no major biases in male quality between male incubation classes. We found no evidence for such differences in three relevant aspects of male quality (Table 2) and found seemingly random changes between incubation statuses of the same individuals between years. These results indicate that our comparison of incubation status was made with a reasonably random sample of males. Many of our non-incubating males may have been generated by very early depredation of nests. Temminck's stints and other small uniparental shorebirds primarily rely on crypsis rather than active defense of nests (Koivula and Rönkä 1998; Smith et al. 2007; Smith and Wilson 2010), and nest loss may not be strongly associated with male quality. To the extent that non-incubators may be biased toward lower quality birds, we will have underestimated the benefits that non-incubators might obtain by pursuing this strategy. On the other hand, if a few high-quality males pursue a non-incubation strategy (see below), these might offset such a bias.

Our study is observational, yet high nest predation rates combined with the fact that we protected a half of the nests early in the season provide an experimental aspect to the generation of incubating versus non-incubating males. This also creates an experimental aspect to the nests that were available to be sampled, as nest protection halved nest predation rates. Due largely to this nest protection and human disturbance, we believe it is reasonable to assume no major bias with respect to incubator/non-incubator status between sampled and unsampled nests. In addition, we missed very few nests during a season. For example, only <6 % of the 153 nests were found at the brood stage.

The social environment differently impacted the fertilization success of each incubation class (Fig. 2). Non-incubator fertilization success increased significantly at lower sex ratios (higher proportions of females). In contrast, while incubators also gained increased fertilization success at lower sex ratios, this response was significantly weaker. Males may cue on the abundance of females early in the season, and conditional reproductive tactics could partly be determined by site sex ratios (Székely et al. 1999; Thomas et al. 2007). From a behavioral perspective of within species variation, these data

support theoretical predictions of the influence of adult sex ratios in the evolution of breeding systems with predominantly female through to male parental care (McNamara et al. 2000; Kokko and Jennions 2008) and would be expected from the comparative studies of shorebirds (Liker et al. 2013). Our study also provides field data supporting recent suggestions of the importance of other individuals in the population in explaining reproductive tactics and breeding behavior (Donald 2007) and how sex ratios may influence the outcome of sexual conflict (Alonso 2009).

This study was conducted in a declining population (Koivula et al. 2008). Sex ratios may become skewed in small populations due to demographic stochasticity (Donald 2011), and our results may not be applicable to larger stable populations. However, sex ratios estimated from our color ringed population have been male-biased throughout our study of the species at this site, being 0.71 on average (range 0.61–0.81) across the 8 years prior (1994–2002) to the current study. These ratios do not include the reconstructions of transient individuals, mainly of females, that the genotyping of offspring has allowed, which reduce the biases substantially (e.g., Fig. 2). The large number of female transients confirms that many females laid clutches, but left our lowland study sites prior to capture and banding. In Hildén's (1975) more stable population, male-biased field sex ratios were also observed. In contrast, strongly female-biased nesting occurred at an alpine site in Norway, due to an influx of later-nesting females, perhaps laying their second clutches (Breiehagen 1989). Such females would be representative of the emigrants from populations similar to ours.

In our study, a few non-incubators gained many fertilizations during a season, despite being incubators in other years. These may be high-quality individuals that in some seasons cue on the social environment and can gain high numbers of fertilizations in the absence of assuming the costs of care. For the most part, Temminck's stint males appear to use a "mixed reproductive strategy" (sensu Trivers 1972) or a "conditional strategy" composed of both parental and mating tactics (sensu Gross 1996, but allowing for some genetic variation (Schuster and Wade 2003)). Being an incubator appears to be the more productive tactic in general, with non-incubating being an alternative tactic adopted by males which, for whatever reasons, do not obtain or lose clutches early in a season. These males are then free to invest more heavily in mating effort, which appears at that point to be their better option, particularly later in the season.

Distinct male reproductive strategies are rare in birds and known in shorebirds only for ruffs (Lank et al. 1995; Jukema and Piersma 2006; Krüger 2008). However, observational and genetic evidence leave open the possibility that some individual males consistently avoid parental care. Unincubated Temminck's stint clutches (two in this study in the 2012 season, see Hildén 1975) are likely those for which a male

did not accept parental duties, reflecting the strong sexual conflict at this stage in this system (Emlen and Oring 1977; Pienkowski and Greenwood 1979; Székely et al. 2007). Detailed observations during 2012 confirmed that one male actively avoided incubation of two nests that were laid following mating. This male displayed for a long period of time and attracted two females that laid and incubated the clutches, but only took on parental duties late in the season, making this brood not entirely "free of care." Ironically, the site sex ratio of 0.77 was the most male-biased encountered in this study and according to Fig. 2 would actually disfavor the non-incubation tactic this male demonstrated. The "parental care opportunity" cost of abandonment is large, but it will be less when (1) the free of care mating opportunities are higher (e.g., Fig. 2), or the male's chances of successfully completing incubation were lower, due to, e.g., harsh environmental conditions. We have evidence of an effect of the former on relative success, but no information about condition-dependent behavior with respect to the latter.

The Temminck's stint system as described by Hildén (1975, see "Introduction") captures the basic aspects of male and female breeding behavior. But within this framework, both sexes pursue complex mating and parental care strategies that include the potential for individual's to mate multiple times with extensive sexual conflict over parental care. Given probable time and physiological constraints, two clutches are likely close to the maximum for most individuals. Temminck's stint males in general employ a mixed reproductive strategy of parental effort and mating effort, with relative success conditional on the sex ratio of the local population. We quantified the Temminck's stint males' additional mating opportunity cost as a loss of ca. 0.13–0.25 of annual potential reproductive output, as estimated by numbers of fertilizations. The proportional costs of providing care in other species will depend on many factors, and it will be interesting to see what emerges as additional estimates become available.

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