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ORIGINAL ARTICLE

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male or males attempting to fertilize a female's eggs do not have all the characteristics beneficial to her or her young (Birkhead and Møller 1996; Møller 2000; Griffith et al. 2002; Westneat and Stewart 2003).

Predicting the outcome of this interaction is complicated by overlaying social opportunities, ecological limitations, and the relative "leverage" of each sex at particular reproductive stages (Brown et al. 1997). For example, territorial behavior may limit mating opportunities for females if females obtain most of the resources they need on the social mate's territory (Birkhead and Møller 1992), but in situations where they leave the territory, extra-pair paternity (EPP) may be quite high (Kempenaers et al. 1992; Smiseth and Amundsen 1995). Mate-guarding can reduce EPP risk (Møller and Birkhead 1993; Westneat 1994; Komdeur et al. 1999), but females may escape their mate's guarding (Johnsen et al. 1998), especially in dense cover (Davies 1992; Mays 2001). Males can increase paternity assurance by increased copulation rates (Birkhead and Møller 1992), but strategic timing of an extra-pair copulation (EPC) can be effective because one EPC can have a higher sperm count than a within-pair copulation (Michl et al. 2002; Pizzari et al. 2003). Social polygyny can affect the interactions between the sexes in ternity assurance should be required for male-only parental care (Ketterson and Nolan 1994; Møller 2000); (2) second clutches should have higher rates of EPP than first clutches, due to stored sperm and rapid mate-switching (Oring et al. 1992); (3) because this is a non-territorial species, paired males should mate guard to prevent copulations from competitors (Birkhead and Møller 1992); (4) males should protect their paternity with elevated copulation attempts and rates (Birkhead and Møller 1992), because the increasing time they spend in nest platform construction precludes continuous mate guarding; second males might be particularly like to use this tactic, to prevent fertilizations from stored sperm; (5) infertility rates should be lower in second clutches, in which increased sperm competition is expected; and (6) males should pursue a mixed reproductive strategy (Trivers 1972) through increased within-pair copulations with their females just prior to clutch completion and through copulations with females seeking second mates (Fitch and Shugart 1984).

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Field methods

Fieldwork was carried out at Cape Espenberg (66 30 N, 163 30 W), on the northern Seward Peninsula, in western Alaska, during late May through mid-July 1977–1979 and 1994–1999. The habitat consisted of wet coastal tundra, interspersed with small ponds and wet sedge marsh, where phalaropes nest and rear young during the short arctic summer (Schamel and Tracy 1987). We searched a 2-km

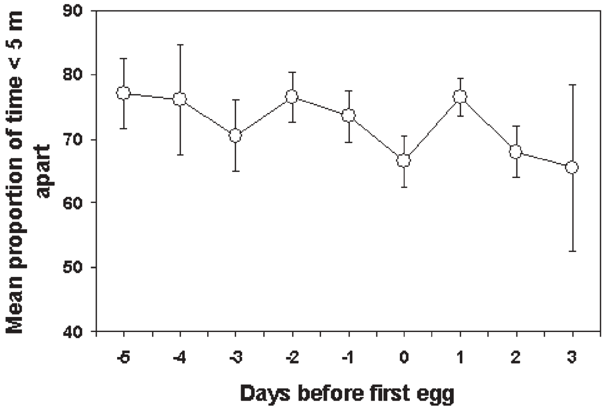

Fig. 2 Proportion of time red-necked phalarope pair members were within 5 m. Mean€SE, day 0 = first egg laid

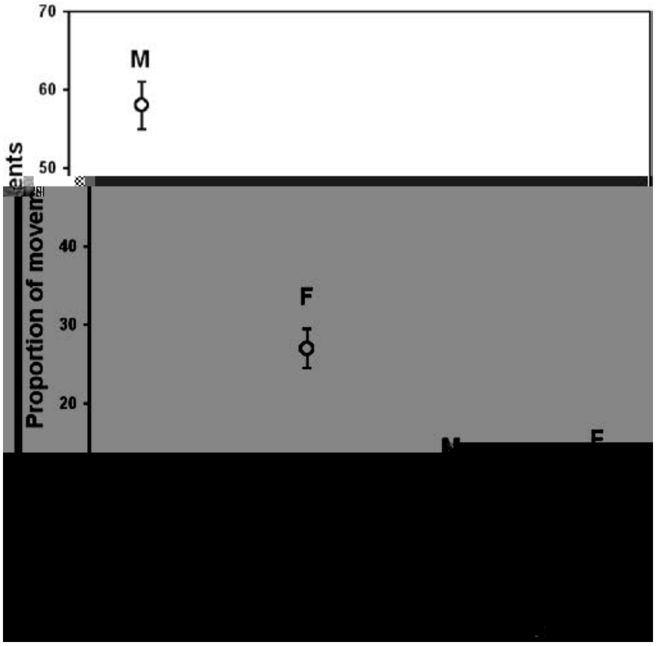

Fig. 3 Proportion of observations in which red-necked phalarope pair member moved toward or away from partner. Mean€SE

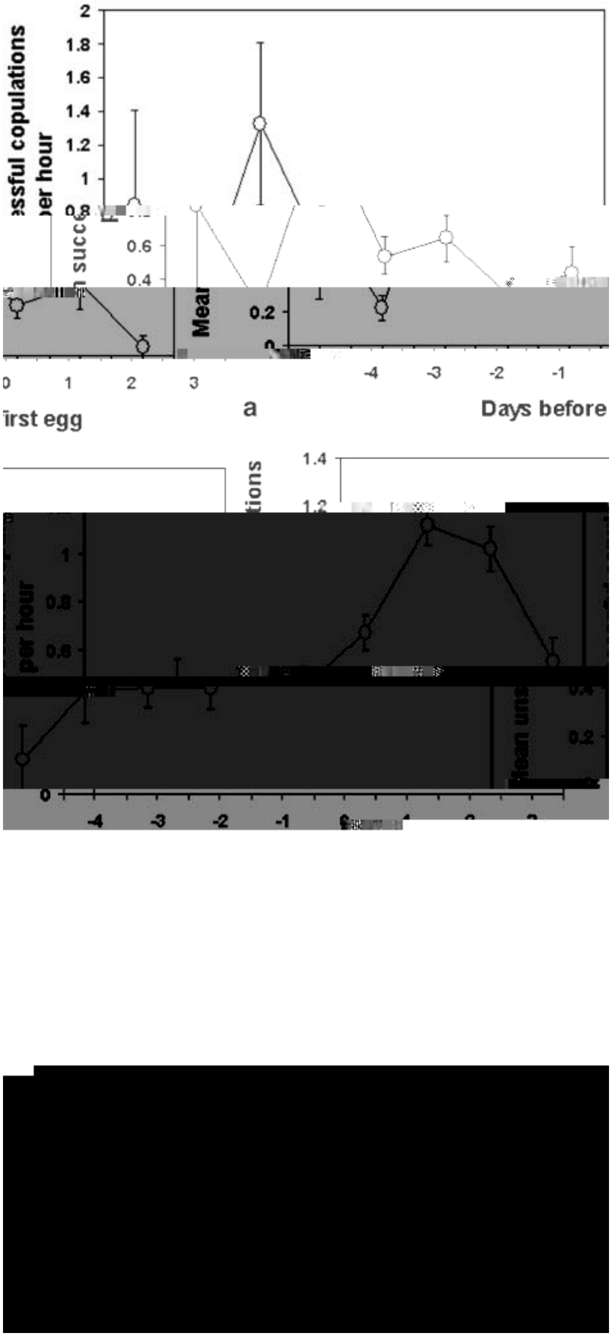

Fig. 4a–c Patterns of within-pair copulation of red-necked phalaropes, with respect to laying stage. a Rate of successful copulation, b rate of unsuccessful copulation, c proportion of attempts that were successful. In all panels, the mean€SE is shown

P<0.0001, n=45 pairs; Bonferroni P <0.05 for each significant contrast). Females and second males stayed within 5 m more often than first/renesting pairs (t-test, t_{43}=2.43, P=0.02; mean=81.8€2.9%, n=18, versus 72.5€2.4%, n=63).

Within-pair copulations

We recorded 178 successful (mean=0.55€0.08/h) and 187 unsuccessful (mean=0.63€0.07/h) within-pair copulations during focal pair observations (n=227 days with observations). Successful copulation rates varied significantly by laying stage (Fig. 4a; one-way ANOVA, $F_{7,194}$=2.07, P=0.048). Laying stage –2 differed significantly from laying stages –3, 1, 2, 3 (Bonferroni adjustment; P<0.05); laying stage 3 differed significantly from laying stage –1 and 0 (Bonferroni adjustment; P<0.05).

Successful copulation rates varied among known clutch types (first, polyandrous, replacement), being higher in renesting pairs than either first (one-way ANOVA, $F_{2,152}$=2.98, P=0.05; contrasts test first versus renest, F=4.96, P=0.03) or polyandrous pairs (contrasts test first vs second, F=3.89, P=0.05). Unsuccessful copulation rates did not differ by clutch type (one-way ANOVA, $F_{2,152}=2.38$, $P=0.10$). Unsuccessful copulation rates varied significantly by laying stage (Fig. 4b; one-way ANOVA, $F_{7,194}=2.43$, $P=0.02$), being significantly higher during the production of eggs 2 and 3 than during prelaying or the production of the first egg (Bonferroni adjustment; $P<0.05$). The percentage of copulations that were successful varied by laying stage (Fig. 4c; repeated measures ANOVA, $F_{7,130}=3.56$, $P=0.001$); percent successful copulations were lower during the production of eggs 2–4 than during the 2 days prior to the production of the first egg (Bonferroni adjustment; all comparisons $P<0.05$).

Extra-pair copulations

We recorded seven successful EPCs during 337.7 h of focal pair observations (0.02/h) and 53 unsuccessful EPCs (0.16/h). None of these copulations involved previous mates. With-in pair copulation attempts were thus substantially more likely to be successful than extra-pair attempts (48%, n=365 copulation attempts vs 12%, n=60 copulation attempts, $X^2=27.8$, $P<0.0001$). Attempted EPCs occurred throughout the nesting season (mean= 16.6€1.0 days after the first egg in the population; range=30 May–27 June), but successful EPCs occurred only after the middle of the season (mean=17.4 days after the first egg in the population; range=11–22 June). Unsuccssful EPCs came primarily from paired, but prelaying, or incubating males (73.6% paired/prelaying; 9.4% incubating; 17.0% unknown status) whose own nests were from 4 days before laying to early incubation. All successful EPCs from males occurred after the male had received the first egg of his clutch. Unsuccessful EPCs focused primarily on paired/laying or post-laying females (54.7% paired/laying; 7.5% post-laying; 37.8% unknown status) from 3 days prior to laying the first egg in a clutch to early post-laying, but primarily during egg-laying. Successful EPCs occurred during late laying.

Infertile eggs

Because we collected eggs for the study, we were able to

Our results also help interpret previously published results of paternity in red and Wilson’s phalaropes. Given

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