Using a Transponder System to Monitor Incubation Routines of Snowy Plovers (Usando un sistema de transpondor para monitorear las rutinas de anidaje de Charadrius a. alexandrinus)

Author(s): András Kosztolányi and Tamás Székely

Source: *Journal of Field Ornithology* , Spring, 2002, Vol. 73, No. 2 (Spring, 2002), pp. 199-205

Published by: Wiley on behalf of Association of Field Ornithologists

Stable URL: https://www.jstor.org/stable/4131146

J. Field Ornithol. 73(2):199–205, 2002

Using a transponder system to monitor incubation routines of Snowy Plovers

András Kosztolányi[1,3] and Tamás Székely[2]

[1] *Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4010 Debrecen, Hungary*
[2] *Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, United Kingdom*

Received 9 January 2001; accepted 13 June 2001

ABSTRACT. We investigated the incubation behavior of a ground-nesting shorebird, the Snowy Plover (*Charadrius a. alexandrinus*) by developing a transponder system that recorded the identity of parents on their nest over 24 h. The system consisted of a small chip glued on the tail of the parent, an antenna that was buried under the nest, and a recording device that was buried nearby. The transponder system was both accurate and reliable, since only 0.2% of records were false. The records of the transponder system were augmented by visual observations, and these data were analyzed by randomization tests. We found strong daily incubation routines: females incubated during the day, whereas males incubated mostly at night. Overall, the females spent significantly more time incubating the nest (11.3 h (median)/day) than the males (9.4 h/day). We discuss several hypotheses for the observed daily incubation routines of the sexes, and propose experimental studies to test these hypotheses.

SINOPSIS. **Usando un sistema de transpondor para monitorear las rutinas de anidaje de *Charadrius a. alexandrinus***

Investigamos la conducta de incubación de un ave costera que anida en el suelo (*Charadrius a. alexandrinus*) al desarrollar un sistema de transpondor que registró la identidad de los padres en su nido por unas 24 horas. El sistema consiste de un pequeño sensor engomado a la cola del padre, una antena enterrada bajo el nido y una máquina de grabación que se enterró cerca. El sistema transpondor fué tán preciso como confiable. Solo cerca del 0.2% de los registros fué falso. Los registros del sistema de transpondor se incrementaron con observaciones visuales, y esos datos se analizaron mediante pruebas al azar. Hallamos rutinas diarias de incubación: las hembras incubaron durante el día mientras que los machos incubaron mayormente de noche. En general, las hembras invirtieron más tiempo incubando en el nido (mediana = 11.3 hrs/dia) que los machos (9.4 hrs/dia). Discutimos varias hipótesis para las rutinas de los sexos de incubación diarias observadas en ambos sexos, y proponemos estudios experimentales para probar estas hipótesis.

Key words: automatic recording, *Charadrius*, daily routines, parental care, sexual conflict, shorebirds

Shorebirds are ideal model organisms to investigate reproductive behavior, because they have a high variety of care patterns including incubation by both parents, only by the male, and only by the female (reviewed by Erckmann 1983; Oring 1986; Reynolds and Székely 1997). Even in shorebirds with biparental care, there is substantial variation between the sexes. For example, males and females share incubation duties approximately equally in European Golden-Plovers (*Pluvialis apricaria*), Black Oystercatchers (*Haematopus bachmani*), and Purple Sandpipers (*Calidris maritima*; Byrkjedal 1985; Purdy and Miller 1988; Pierce 1997), whereas most incubation is carried out by the female in Northern Lapwings (*Vanellus vanellus*; Parish and Coulson 1998; Liker and Székely 1999).

We investigated the incubation routines of a ground-nesting precocial shorebird, the Snowy Plover (*Charadrius a. alexandrinus*). Although brood-rearing behavior of Snowy Plovers has been extensively studied recently (Paton 1995; Fraga and Amat 1996; Székely and Cuthill 1999), their incubation behavior, especially nighttime incubation, is poorly understood. For example, previous investigations of incubation were carried out only in daytime (Purdue 1976; Nakazawa 1979; Paton 1995), and thus they do not provide unbiased information on the relative contribution of each sex.

The objective of our study was to investigate the daily routines of incubation by male and

[3] Corresponding author. Current address: Department of Ecology, Institute for Zoology, Faculty of Veterinary Science, Szent István University, H-1400 Budapest, Pf. 2. Hungary. Email: <koszti3@falco.geobio.elte.hu>

female Snowy Plovers during both daytime and at night. To achieve this objective, we developed an automatic recording device (the "transponder system"). Although transponders are commonly applied in avian field studies to monitor survival (e.g., Becker and Wendeln 1997; Carver et al. 1999), our transponder system was developed and used to record incubation in a ground-nesting species.

STUDY SITE AND METHODS

Fieldwork was carried out at Lake Tuzla (36°43′N, 35°03′E), southern Turkey. Approximately 1000 pairs of Snowy Plovers bred in the saltmarsh around the lake (Székely and Cuthill 1999). Most of the vegetation was comprised of halophytic plants, such as *Artrochnemum fruticosum*, *Salicornia europaea*, and *Sueda prostrata* (Uzun et al. 1995). The study was carried out in an area of approximately 52 ha on the north side of the lake over three years (15 April–30 June 1997; 1 May–20 June 1998; 15 April–20 June 1999).

Both parents were caught on their nest by funnel traps, and banded with a metal band and an individual combination of color bands. The plumage of males and females is sufficiently dimorphic to allow the identification of the sexes. Behavioral records were collected only after the clutch was completed and the incubation had commenced. Only clutches of three eggs (the modal clutch size, Székely et al. 1994) were investigated.

We used two methods to record the behavior of parents at their nest.

The transponder system. An automatic recording system was developed and used in 1997 to determine which parent incubated the eggs. First, we caught both parents on the same day or on subsequent days, and glued a 0.4 g plastic-coated passive chip (wedge-shaped TIRIS read-only transponder, Texas Instruments, U.S.A.) on the tail feathers of each parent using Araldite glue (Evode Ltd., U.K.). Gluing the transponder took approximately 15 min. Each transponder had a unique identification code. Each transponder weighed about 1% of the adult body mass. Second, a circular antenna with a diameter of 9.5 cm was buried approximately 0.5 cm deep under the nest. To bury the antenna, we removed the complete nest including the eggs and the nest material, and once the antenna was in position we put the nest back. The antenna was made of ceramic-coated wire, and it was connected to a TIRIS Micro-reader. The reader was connected to a palmtop computer (PSION Organiser II) that controlled the reader and collected the data. The reader and the computer were enclosed in a box and buried approximately 0.5 m from the nest. Third, a car battery (12 V), which powered both the reader and the palmtop computer, was buried approximately 5 m from the nest. The installation of the system took about 45 min. The installation was carried out early in the morning or late afternoon to minimize the impact of heat on the eggs. It is unlikely that the presence of the transponder system disturbed the parents, since all units of the system, including the cables, were hidden underground. The parents returned to the nest in a few minutes once the installation was complete.

Every 20 s the system read whether the male, the female, or neither parent was on the nest, and it stored the date, time, and the identity of the parent if it was different from the previous record. If the system was unable to identify the transponder, then the record was stored as false. The system was able to record and store data for several weeks without interruption. Nevertheless, we checked it every day for proper operation. Each nest was recorded for at least 24 h. The parents lost the transponder by molting their tail feathers after the breeding season, as confirmed by four plovers that were fitted with a transponder in 1997 and recaptured in 1998.

Observations. The behavior of parents was also monitored from a blind at about 45–70 m from the nest using instantaneous sampling. Between 06:00 and 21:00 (local time, i.e., GMT + 3 h), we recorded which parent (if any) incubated the nest every 30 s for two hours (in 1997), or every 20 s for two or three hours (in 1998 and 1999). All observations were carried out by AK.

To assess the reliability of the transponder system, data were collected simultaneously by both the transponder system and direct observations at five nests. During these observations the timing of the scans was synchronized with the system clock of the transponder system. No nest was abandoned due to capture or installment of the transponder system.

Table 1. Laying data and incubation stage of nests under study (N = 22 in 1997, 24 in 1998, 40 in 1999). Laying date is the number of days since 1 January, and incubation stage is the number of days for which the clutch had been incubated at the time of behavioral records.

Year	Mean ± SE laying date (range)	Mean ± SE incubation state (range)
1997	138.4 ± 3.3 (116–175)	14.3 ± 1.1 (1–23)
1998	140.9 ± 2.7 (115–162)	9.8 ± 0.9 (4–19)
1999	136.4 ± 2.6 (105–164)	8.9 ± 0.7 (3–21)

STATISTICAL ANALYSES

We considered each nest as the unit of analysis (Table 1). If more than one nest was available for an individual (for instance, the plover laid a replacement nest or bred in several years), we used the nesting attempt for which we had the most records.

The reliability of the transponder system. We used two variables to assess the reliability of the transponder system: (i) total incubation time (%), that is the percentage of observations when the clutch was incubated by either parent; and (ii) incubation by the female (%), that is the percentage of total incubation time when the female incubated the clutch. If several visual observations were available for a parent, we used the mean of these observations.

Daily routine of incubation. Each day was divided into eight intervals of three hours each. Four variables were evaluated for these intervals: (i) total incubation time (%), (ii) incubation by the female (%), (iii) duration of male incubation, and (iv) duration of female incubation. For the first two variables, only the records that lasted for at least one hour in a given interval were included. The latter two variables were defined as the time that elapsed from the beginning of incubation by a given parent until the parent left the nest and the incubation was taken over by the other parent. Only those durations were included in the analyses in which both the beginning and the end of the incubation by a given parent were recorded. Each duration was assigned to the interval in which the incubation by that parent began. If several records were available for an individual in an interval, then the mean of these records for that interval was used. Incubation behavior was not different between years (two-way ANOVAs; total incubation time, year: $F_{2,74} = 1.404$, $P = 0.252$; time of day: $F_{3,74} = 9.068$, $P < 0.001$; interaction: $F_{6,74} = 1.388$, $P = 0.231$; incubation by the female, year: $F_{2,74} = 0.261$, $P = 0.771$; time of day: $F_{3,74} = 6.381$, $P = 0.001$; interaction: $F_{6,74} = 0.444$, $P = 0.847$).

Repeated observations of the same individual are not independent from each other. To control for this source of error, the daily activity was analyzed in two ways. (i) We used repeated-measures ANOVA in which time of day was the within-subject factor. Percentage variables were arcsine transformed, whereas the durations of incubation were $\log_{10}(x)$ transformed. In repeated-measures ANOVA, we used only the transponder data, because it requires data in all intervals for a given nest. For the duration of incubation by either the male or the female, we had few data at night because change-overs were rare (see Results). Therefore, we kept the number of nests over four by excluding some intervals. (ii) We also investigated the daily activity using randomization tests (Manly 1997), in which data collected by either observations or the transponder system were included. Between-group sum of squares was used as a test statistic and the number of rearrangement was $10^5 - 1$. The randomization was carried out separately for each nest (stratified shuffling, Noreen 1989), i.e., only one record of a given nest was allocated to a given interval.

Statistical analyses were carried out using SPSS for Windows 8.0 (Norušis 1994). We provide the number of nests (N) and two-tailed probabilities. Medians (lower quartiles–upper quartiles) are given, unless otherwise stated.

RESULTS

The reliability of the transponder system. The transponder system was both reliable and accurate in the field. The percentage of false readings was 0.2% of total recording time, and 96.0% of false readings lasted for only 20 s. The data collected simultaneously by an observer and the transponder system (dependent variable) were highly correlated, and the slopes of linear regressions were not different from one (Pearson correlations, total incubation time: $r = 0.996$, $N = 5$, $P < 0.001$; incubation by the female: $r = 1.000$, $N = 5$,

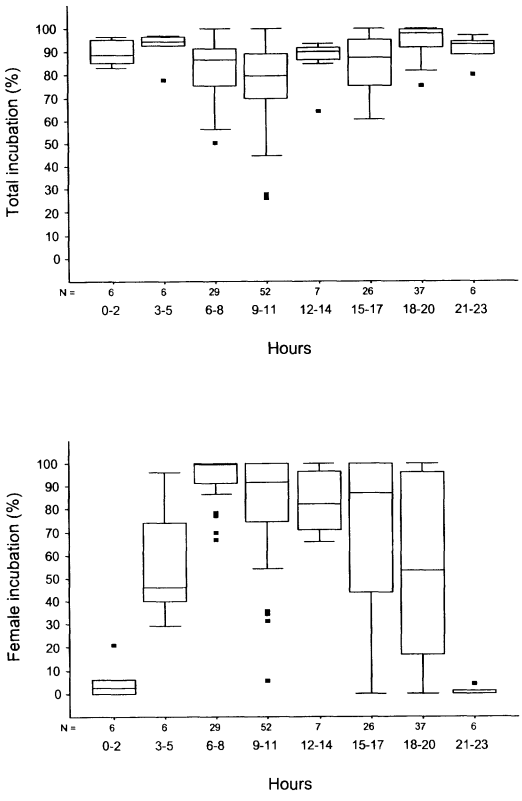

Fig. 1. (upper) Total incubation time (%), and (lower) incubation by the female (%) over the day (N = 86 nests, 1099 total hours). Medians, interquartile ranges (boxes), lowest and highest observations (whiskers) within the range of LQ − 1.5*(UQ − LQ) and UQ + 1.5*(UQ − LQ), and outliers (squares) are given, where LQ is the lower quartile and UQ is the upper quartile.

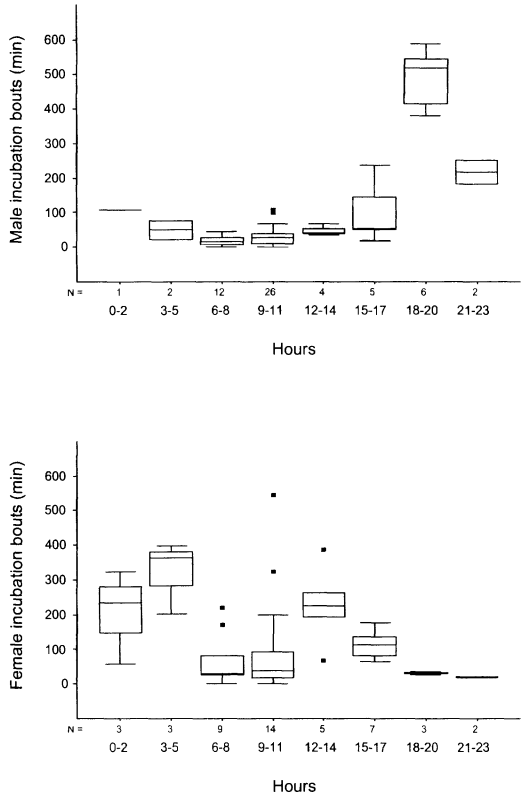

Fig. 2. (upper) Duration of incubation bouts by males (N = 32 nests, 908 total hours), and (lower) by females (N = 18 nests, 840 total hours) over the day. See Fig. 1 for legend. Incubation bouts are given for the time period in which they started.

$P < 0.001$; t-tests on the slopes, total incubation time: $b = 0.974$, $t_3 = 0.515$, $P = 0.642$; incubation by the female: $b = 1.008$, $t_3 = 0.585$, $P = 0.600$).

Daily routine of incubation. Eggs were incubated for 89.4% (86.8%–94.0%) of the day by one or the other parent. Total incubation time was lowest between 09:00 and 12:00 (median: 79.7%), whereas it was highest between 18:00 and 21:00 (median: 98.0%, Fig. 1, upper). Total incubation time varied significantly over the day (ANOVA, $F_{7,35} = 6.190$, $N = 6$, $P < 0.001$; randomization, $N = 86$, $P < 0.001$).

Females provided 68.0% (13.5%–90.9%) of total incubation (Fig. 1, lower). The share of incubation between the sexes varied significantly over the day (ANOVA, $F_{7,35} = 32.698$, $N = 6$, $P < 0.001$; randomization, $N = 86$, $P < 0.001$), since females spent more time incubating nests than males between 06:00 and 21:00 (Wilcoxon matched-pairs test, $Z = 5.495$, $N = 86$, $P < 0.001$, Fig. 1, lower), whereas nearly all incubation was performed by males between 21:00 and 06:00 (Wilcoxon matched-pairs test, $Z = 2.201$, $N = 6$, $P = 0.031$, Fig. 1, lower). Overall, females spent more time incubating the nest (11.3 h/day (10.2–11.8 h/day)) than males (9.4 h/day (9.1–9.8 h/day); Wilcoxon matched-pairs test, $Z = 2.201$, $N = 6$, $P = 0.031$).

Duration of incubation bouts. The duration of incubation bouts of males was 50.2 min (29.1–188.7 min). Males often incubated eggs throughout the night without being relieved (Fig. 2, upper), whereas they incubated for short periods during the day (ANOVA, $F_{3,9}$

= 40.033, $N = 4$, $P < 0.001$; randomization, $N = 32$, $P < 0.001$).

The duration of incubation bouts of females was 75.3 min (30.2–231.0 min, Fig. 2, lower). We found no variation in female bouts between 06:00 and 18:00 (ANOVA, $F_{3,12} = 2.049$, $N = 5$, $P = 0.161$), although over the whole day there was significant variation (randomization, $N = 18$, $P = 0.018$).

DISCUSSION

The reliability of the transponder system. The transponder system was very reliable: the percentage of false readings was low and the correlation between the observations and the transponder data was high. This system is relatively cheap, since it costs USD 550–600 and one transponder is about USD 5. Therefore, we recommend this system for studying incubation routines, particularly in ground-nesting birds (e.g., waterfowl, grouse, and shorebirds).

We recommend checking the operation of the system on a daily basis, since we had a few cases when the system failed to record due to the corrosion of the antenna in the highly saline environment. False readings were rare, and they probably occurred when one parent was just about to settle on the eggs, or had just left, since the reading range of the antenna was small (10–20 cm), and the ability of the receiver to read the code of the transponder depended upon the angle between the antenna and the transponder.

Although the transponder system was precise, we identified three limitations. First, it is unable to distinguish between shading the eggs and true incubation. Shading of the eggs occurs at high ambient temperatures in the Snowy Plover (Nakazawa 1979). Second, the system did not record when an untagged bird incubated the nest. For instance, in 1997 we tagged one male and one female at a nest, and later we also observed a second, untagged female incubating at this nest (this nest was not included in the current study). Incubation of a single nest by two females is very unusual in the Snowy Plover (Cramp and Simmons 1983). Third, humidity and a salty environment may damage the transponder system causing corrosion and electric shortcuts. To avoid these problems the antenna should be properly coated, and the system should be enclosed in watertight boxes. Watertight containers are also important to avoid flooding.

Daily routine of incubation. The percentage of time spent by one or the other parent on the eggs was high throughout the day, although we still detected a significant daily variation. The highest percentage of incubation occurred at night, in early morning, and at midday. These results agree with previous observations that incubation is most intensive when the ambient temperature is extremely cold or hot (Purdue 1976; Nakazawa 1979).

Our study overcomes two limitations of previous studies in Snowy Plovers (Purdue 1976; Nakazawa 1979; Paton 1995). First, in these studies the behavior of parents was investigated only during the daylight period; thus it was not known which sex (if any) incubated at night. Full 24-h records are important, for example, to reveal the contribution of each sex to total care provisioning. Second, some of the previous studies did not use appropriate statistical tests. For example, Purdue (1976) assumed that each of his observations was independent. Clearly, this was not the case, and appropriate statistical tests such as repeated-measures ANOVA and randomization tests are required to avoid pseudoreplication.

In several plovers such as the Wilson's Plover (*Charadrius wilsonia*), Killdeer (*Charadrius vociferus*), Semipalmated Plover (*Charadrius semipalmatus*), and Snowy Plover, the female incubates mostly during the day, whereas the male incubates at night (Thibault and McNeil 1995; Warnock and Oring 1996; Blanken and Nol 1998; this study). We propose four reasons for the different daily routines of males and females. First, females may forage at night to recover their energy deficit, especially shortly after egg-laying (Staine and Burger 1994). Therefore, males (that are not exhausted by egg-laying) are able to spend the night on the nest, whereas the females may need to forage. However, this hypothesis is unlikely to explain incubation routines in our study, since in our population the plovers rarely feed at night (A. Kosztolányi and T. Székely, pers. obs.). Second, the male may have to defend the territory during daytime, which restricts his ability to help his mate incubate. However, Snowy Plovers do not maintain territories around their nest at our study site (A. Kosztolányi and T. Székely, pers.

obs.). Third, male Snowy Plovers have black breast-bands and head-stripes, and cinnamon crowns, whereas the females are pale brown. Therefore, the more colorful male may be more conspicuous to visually searching predators than the dull female, and thus males may be more likely to give away the location of the nest during daytime. Fourth, males and females may have different abilities to detect predators approaching the nest. Wilson's Plovers sit motionless on the nest during daytime, but they scan all directions to detect predators at night (Thibault and McNeil 1995). If males are better at detecting the predators at night than females, for instance, because they may have better eyesight, then they may be able to leave the nest earlier than females if a predator approaches. We conclude that the first two explanations are unlikely at our study site, whereas the latter two warrant further investigation.

Incubation bouts of males were long at night, whereas females had much shorter bouts. These observations suggest that males are more persistent incubators than females. Females presumably have depleted energy reserves due to egg-laying (e.g., Thibault and McNeil 1995), and thus they may not be able to undertake the whole daylight incubation without interruption.

In conclusion, we recommend the transponder system to record incubation behavior in ground-nesting birds. Our experiences were positive since the transponder system was both accurate and reliable. We also showed that male and female Snowy Plovers have different daily incubation routines. Such a difference may emerge if the costs or the benefits of incubation vary over the day. Future observations on the daily routines, and experimental manipulations of males and females, will be important to determine how these costs and benefits influence incubation behavior, and whether the male or the female drive the observed incubation patterns.

ACKNOWLEDGMENTS

We thank J. Kis, Á. Lendvai, I. Szentirmai, and Y. Demirhan for help in the field. T. Yilmaz and Ö. Karabacak helped us overcome difficulties in logistics. J. Reiczigel and Z. Barta helped us with statistical analyses. We thank Computer Praxis Ltd. for their assistance in using transponders. Permission for fieldwork was provided by the Turkish Ministry of National Parks, Tuzla Municipality and the Governor of Karatas (Mr E. Karakaya). Rings were provided by Radolfzell Vogelwarte (Germany) and Professor P. R. Evans. The study is part of the Ph.D. fellowship of AK, and it was supported by grants from the Hungarian Scientific Research Fund (OTKA T031706), the Hungarian Ministry of Education (FKFP-0470/200), and NERC (GR3/10957). We thank A. I. Houston, J. M. C. Hutchinson, and R. J. Thomas for their comments on previous versions of the manuscript.

LITERATURE CITED

BECKER, P. H., AND H. WENDELN. 1997. A new application for transponders in population ecology of the Common Tern. Condor 99: 534–538.

BLANKEN, M. S., AND E. NOL. 1998. Factors affecting parental behavior in Semipalmated Plovers. Auk 115: 166–174.

BYRKJEDAL, I. 1985. Time-activity budget for breeding Greater Golden-Plovers in Norwegian mountains. Wilson Bulletin 97: 486–501.

CARVER, A. V., L. W. BURGER, JR., AND L. A. BRENNAN. 1999. Passive integrated transponders and patagial tag markers for Northern Bobwhite chicks. Journal of Wildlife Management 63: 162–166.

CRAMP, S., AND K. E. L. SIMMONS. 1983. The birds of the Western Palearctic, vol. 3. Oxford University Press, Oxford, UK.

ERCKMANN, W. J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: Social behavior of female vertebrates (S. K. Wasser, ed.), pp. 113–168. Academic Press, New York.

FRAGA, R. M., AND J. A. AMAT. 1996. Breeding biology of a Kentish Plover (*Charadrius alexandrinus*) population in an inland saline lake. Ardeola 43: 69–85.

LIKER, A., AND T. SZÉKELY. 1999. Parental behaviour in the Lapwing *Vanellus vanellus*. Ibis 141: 608–614.

MANLY, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd ed. Chapman and Hall, London.

NAKAZAWA, R. 1979. Incubation behaviour of the Kentish Plover, *Charadrius alexandrinus*, with special reference to the share of sexes and effect of ground surface temperature. Miscellaneous Reports of the Yamashina Institute of Ornithology 11: 54–63.

NOREEN, E. 1989. Computer-intensive methods for testing hypotheses: an introduction. Wiley, New York.

NORUŠIS, M. J. 1994. SPSS Advanced Statistics. 6.1. SPSS Inc., Chicago.

ORING, L. W. 1986. Avian polyandry. Current Ornithology 3: 309–351.

PARISH, D. M. B., AND J. C. COULSON. 1998. Parental investment, reproductive success and polygyny in the Lapwing *Vanellus vanellus*. Animal Behaviour 56: 1161–1167.

PATON, P. W. C. 1995. Breeding biology of Snowy Plovers at Great Salt Lake, Utah. Wilson Bulletin 107: 275–288.

PIERCE, E. P. 1997. Sex roles in the monogamous Purple Sandpiper *Calidris maritima* in Svalbard. Ibis 139: 159–169.

PURDUE, J. R. 1976. Thermal environment of the nest

and related parental behavior in Snowy Plovers, *Charadrius alexandrinus*. Condor 78: 180–185.

PURDY, M. A., AND E. H. MILLER. 1988. Time budget and parental behavior of breeding American Black Oystercatchers (*Haematopus bachmani*) in British Columbia. Canadian Journal of Zoology 66: 1742–1751.

REYNOLDS, J. D., AND T. SZÉKELY. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. Behavioral Ecology 8: 126–134.

STAINE, K. J., AND J. BURGER. 1994. Nocturnal foraging behaviour of breeding Piping Plovers (*Charadrius melodus*) in New Jersey. Auk 111: 579–587.

SZÉKELY, T., AND I. C. CUTHILL. 1999. Brood desertion in Kentish Plover: the value of parental care. Behavioral Ecology 10: 191–197.

———, I. KARSAI, AND T. D. WILLIAMS. 1994. Determination of clutch-size in Kentish Plover *Charadrius alexandrinus*. Ibis 136: 341–348.

THIBAULT, M., AND R. MCNEIL. 1995. Day- and nighttime parental investment by incubating Wilson's Plovers in a tropical environment. Canadian Journal of Zoology 73: 879–886.

UZUN, G., M. YÜCEL, K. T. YILMAZ, AND S. BERBEROĞLU. 1995. Biotop mapping in Mediterranean type coastal ecosystems. Proceedings of the Second International Conference on the Mediterranean Coastal Environment, MEDCOAST 95: 131–140.

WARNOCK, N., AND L. W. ORING. 1996. Nocturnal nest attendance of Killdeers: more than meets the eye. Auk 113: 502–504.