

- uador. Ph.D. dissertation, Louisiana State Univ., Baton Rouge.
- TRAVASSOS, L. 1944. Revisao da familia Dicrocoeliidae Odhner, 1910. Monogr. Inst. Oswaldo Cruz Rio 2:1-357.
- TRAVASSOS, L., J. F. T. FREITAS, AND A. KOHN. 1969. Trematodeos do Brasil. Mem. Inst. Oswaldo Cruz Rio 67:1-886.
- YAMAGUTI, S. 1958. Systema Helminthum. I. The digenetic trematodes of vertebrates. Interscience Publishers, New York.

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## Nocturnal Behavior of Breeding Trumpeter Swans

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The study of nocturnal waterfowl behavior has received little attention, in part because researchers have usually assumed night to be a time of little or no activity (Baldassarre et al. 1988, Jorde and Owen 1988, Paulus 1988). The few studies that have focused on nocturnal activity have shown a surprising amount of behavioral variation (Linsell 1969, Nilsson 1970, Swanson and Sargeant 1972, Ydenberg et al. 1984). Waterfowl studies that included evaluations of nighttime activity have revealed a variety of nocturnal behaviors (Raveling et al. 1972, Ebbinge et al. 1975, Tamisier 1976, Pedroli 1982, Aldrich and Raveling 1983, Moulton and Weller 1984, Paulus 1984, Madsen et al. 1989). However, none of these studies focused specifically on nocturnal behavior.

Differences in nocturnal behavior between waterfowl may be due to the great variety of environmental and physiological stimuli encountered by various species (Jorde and Owen 1988). Nilsson (1970), for example, found that three of nine species of diving ducks studied in Sweden were predominantly nocturnal feeders, while the other six were diurnal; nocturnal feeders mostly fed on sessile foods while the diurnal birds ate more mobile prey. Predation pressure is less intense at night and may encourage nocturnal feeding in some ducks (Tamisier 1974, Paulus 1984). Nocturnal feeding also might be important to birds that are energetically stressed, such as prelaying females or birds undergoing wing molt (Jorde and Owen 1988). These examples illustrate the importance of including nocturnal observations when studying a species' behavior and ecology. Conclusions based solely on diurnal data will not represent diel patterns and might lead to a misinterpretation of diurnal activities (Baldassarre et al. 1988, Jorde and Owen 1988).

Nocturnal feeding and other behaviors have been documented in wintering Mute Swans (*Cygnus olor*), Bewick's Swans (*C. columbianus bewickii*), and Trumpeter Swans (*C. buccinator*; Owen and Cadbury 1975, McKelvey and Verbeek 1988). Nocturnal behavior of breeding swans is unknown. Cooper (1979) and Hampton (1981) used electronic monitoring devices (Cooper and Afton 1981) to quantify the presence of incubating female Trumpeter Swans at the nest during the nocturnal period, but nighttime behavior of males, nonincubating females, and cygnets was not evaluated.

We studied the nocturnal behavior of Trumpeter Swans breeding in Wyoming and Idaho in 1991. Our objective was to quantify nocturnal behavior of breeding Trumpeter Swans through direct observations using night-vision equipment. Specific questions addressed were: (1) Are breeding swans active at night? (2) If nocturnal activity is occurring, is it correlated with environmental and physiological factors? (3) What is the relative importance of diurnal and nocturnal periods to breeding swans?

*Methods.*—Staging and breeding swans were observed on wetlands in: Wyoming at Yellowstone National Park; Idaho in the Ashton and Island Park Districts of the Targhee National Forest, in Harriman State Park, and on the Sand Creek State Wildlife Refuge. The ecological aspects of this region have been described by Banko (1960), Shea (1979), and Maj (1983).

Observation blinds were erected at staging areas and on nearby hills that overlooked four swan breeding territories. All blinds were hidden by vegetation and were located 100 to 250 m from the nest mounds. Observations also were recorded from vehicles parked on roads overlooking two other territories. We observed each territory every two to four days from prelaying through brood rearing. We used spotting scopes (60×) by day and Noctron-V Model 9878 light-intensifying night-vision scopes (Varo Inc., Electron Devices Division, Garland, Texas) at night. Night-

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TABLE 1. Mean activity time budgets (in percent) during diurnal and nocturnal observation periods for nonbreeding Trumpeter Swans in Wyoming and Idaho, 1991 (two-tailed unpaired *t*-test, *df* = 27).

Behavior	Day <sup>a</sup>	Night <sup>b</sup>	<i>P</i>
Head-up	17.9	16.8	0.291
Feeding	48.0	21.4	0.003
Preen	30.3	13.7	0.123
Sleep	3.8	48.1	0.0005

<sup>a</sup> 17 birds, 6 days, 313 scans.

<sup>b</sup> 12 birds, 3 nights, 160 scans.

vision scopes were equipped with 135-mm *f*1.8 lenses that provided just under 3× magnification, but optimal light conditions allowed us to substitute 100–300-mm and 600-mm lenses that provided 6× and 12× magnification, respectively. No additional light sources were used to illuminate and monitor birds, except that on occasion a penlight with a red filter was used to initially locate birds on wetlands.

Observation periods were not random due to logistical and access constraints. Nocturnal observations were made under clear to cloudy skies because night-vision scopes do not function well in the rain (Paulus 1984). Optimal conditions occurred under clear skies with some moonlight and, at such times, observation quality approached that of diurnal sessions. During the worst nocturnal conditions, incubating females could only be recorded as on or off the nest; males could not be seen and were recorded as unknown.

Swan behavior was recorded using NEC-8300 portable laptop computers. Birds were sexed by observing copulation and egg-laying behaviors, and individuals were recognized by noting the unique feather stain patterns on the head and neck of each bird (Cooper 1979, Hawkins 1986). Scan observations (Altmann 1974) of swan locations and behaviors were recorded at 6-min intervals. Previous research found no difference in Trumpeter Swan time budgets using both 2-min and 6-min intervals (Grant 1991). Terminology describing incubation recesses, behaviors, and postures was adapted from Lazarus and Inglis (1978), Cooper (1979), and Hawkins (1986). Behavior categories included feeding, head up (alert), preening, nest building, courtship, agonistic interaction, sleeping or resting, incubation, brooding, and other/unknown. Birds sleeping/resting or incubating were considered inactive; all other behaviors were considered active. Continuous observations (Altmann 1974) were used to record feeding-bout length and responses of swans to predators and conspecifics; activities were timed by stopwatch and described into a tape recorder.

A single estimate of activity for each diurnal or nocturnal observation period was calculated as the percentage of scans spent in each behavior during that observation period. Because sampling was un-

equally distributed among swan territories, values were calculated for individual birds by averaging the daily means for each period of the breeding season (i.e. prelaying/laying, incubation, posthatching). Thus, every bird contributed one mean diurnal value and one mean nocturnal value for each statistical test. Mean time-budget data were transformed with an arcsine calculation (Zar 1984). Two-tailed paired *t*-tests (unless otherwise noted in text) were used to evaluate differences between diurnal and nocturnal behaviors, ambient temperatures, frequency of agonistic interactions, types of foraging, and length of feeding bouts.

*Results.*—Observations began on 17 April 1991 and ended 27 July 1991. Swans were scanned 7,791 times during 824 h of observation at six breeding territories and two staging areas. There were 72 nocturnal observation sessions (*n* = 3,963 scans) and 75 diurnal sessions (*n* = 3,828 scans). Most diurnal and nocturnal observation periods lasted at least 3 h, and over half of the nocturnal sessions extended from sunset to sunrise when two observers were available. Length of the nocturnal period decreased from about 9 h in late April to about 7 h during midsummer. Daytime observation temperatures at all six territories ( $\bar{x}$  = 12.8 ± 1.68°C) were warmer than nocturnal temperatures ( $\bar{x}$  = 4.6 ± 1.33°C, *t* = 6.62, *df* = 5, *P* = 0.001). A daily range of 20°C between the high and low temperatures was common, and the lowest nocturnal temperature during observations was –6°C.

Twenty-nine swans were monitored during six diurnal and three nocturnal observation sessions before the spring thaw of breeding areas. Flocks of 100 to 150 birds congregated at staging areas, where birds slept, fed, preened, swam, walked, flew, and engaged in agonistic behavior both day and night (Table 1). Sex and breeding status of staging swans were unknown, but all were probably nonbreeding birds because breeders had left staging areas and were defending territories. Twelve of the 29 birds had gray plumage and were hatched the previous year, and all birds fed in groups of three or more. None was obviously paired.

Trumpeter Swans on breeding territories exhibited a range of nocturnal activities throughout the season. Male swans (*n* = 6) were active for all or part of 53 of 60 (88.3%) nocturnal observation periods and were not observed during the nine remaining sessions. Females (*n* = 6) were active during 34 of 68 (50%) periods and were not observed during one session. Swan pairs hatched cygnets on four of the six nesting territories, and cygnets were active on 10 of 19 (52.6%) nights. One pair did not initiate incubation and may not have laid, while another pair laid and incubated eggs but no eggs hatched successfully.

Time budgets for adult swans were divided into prelaying/laying, incubation, and posthatching periods. Feeding was the predominant diurnal and nocturnal behavior of female and male swans during prelaying (Table 2). Incubating females fed little dur-

ing the day and never at night. None of the five incubating females left their nests during 33 nocturnal observation sessions, while diurnal feeding recesses were relatively common. Male swans reduced their feeding rate during incubation and fed less at night than by day (Table 2). Males often were difficult to observe when inactive during the incubation and posthatching periods, which resulted in a relatively large percentage of unknown observations for these birds (Table 2). Adults of both sexes increased overall feeding activity after the cygnets hatched. Most feeding took place by day, while sleeping and brooding (female only) were most common at night.

Cygnets fed predominantly during the diurnal period (Table 2), but three of the four broods also fed regularly at night. Cygnets less than two weeks old spent an average of  $2.1 \pm 1.2\%$  of their time feeding at night, while those from two to five weeks old spent  $16.1 \pm 6.0\%$  of their time feeding at night ( $t = -2.82$ ,  $df = 3$ ,  $P = 0.067$ ). Diurnal feeding activity for cygnets under two weeks averaged  $34.2 \pm 6.0\%$ , while those from two to five weeks old averaged  $48.9 \pm 4.3\%$  ( $t = -1.24$ ,  $df = 3$ ,  $P = 0.32$ ). Lengths of male diurnal and nocturnal feeding bouts did not differ (diurnal,  $\bar{x} = 43.0 \pm 5.57$  min,  $n = 78$ ; nocturnal,  $\bar{x} = 51.9 \pm 8.88$  min,  $n = 47$ ;  $t = -1.24$ ,  $df = 3$ ,  $P = 0.30$ ), nor did female bouts (diurnal,  $\bar{x} = 50.0 \pm 5.84$  min,  $n = 54$ ; nocturnal,  $\bar{x} = 49.6 \pm 8.96$  min,  $n = 36$ ;  $t = 0.05$ ,  $df = 3$ ,  $P = 0.96$ ). However, cygnet diurnal feeding bouts were almost twice as long as nocturnal bouts (diurnal,  $\bar{x} = 57.5 \pm 7.12$  min,  $n = 23$ ; nocturnal,  $\bar{x} = 30.3 \pm 6.17$  min,  $n = 11$ ;  $t = 5.52$ ,  $df = 2$ ,  $P = 0.031$ ). Swans fed at, above, or below the water surface, and there were no differences between the diurnal and nocturnal periods in relative types of feeding behavior for males, females, or cygnets (all  $P > 0.112$ ).

Adult swans displayed aggressively toward other swans and waterfowl ( $n = 58$ ), especially Canada Geese (*Branta canadensis*,  $n = 33$ ). There was no difference in frequency of agonistic interactions between day and night periods. Nesting swan pairs averaged  $6.8 \pm 3.3$  diurnal agonistic encounters and  $5.0 \pm 1.7$  nocturnal encounters ( $t = 0.772$ ,  $df = 4$ ,  $P = 0.483$ ). Males regularly chased other swans and geese at night, and swans called through the night on several territories. Swans were observed at night in triumph displays ( $n = 4$ ) after successful territorial defense encounters with other swans (see Cooper 1979). Ducks were chased on only three occasions and were usually tolerated by the swans. Feeding swans were regularly accompanied at night by small numbers of American Wigeons (*Mareca americana*), Mallards (*Anas platyrhynchos*), Ring-necked Ducks (*Aythya collaris*), or American Coots (*Fulica americana*). Ducks fed less commonly near swans that had cygnets, but these observations were not quantified. Swan copulations were seen during the day ( $n = 5$ ), but no copulations or other courtship behaviors were seen at night. Courtship and agonistic behaviors comprised a relatively small per-

TABLE 2. Mean activity time budgets (in percent) during diurnal (D) and nocturnal (N) observation periods for Trumpeter Swans during three periods of breeding season in Wyoming and Idaho, 1991 (two-tailed paired *t*-test).

Mean (%) <sup>a</sup>	Head-up		Feeding		Nest building		Preen		Sleep		Incubation <sup>b</sup>		Other/unknown		
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	
Prelaying/laying Incubation Posthatching	9.4	5.3	70.0	72.5	2.9	0.10	7.1	4.9	9.5	12.6	—	—	1.1	4.6	
	6.6	**	0.2	9.0	*	0	2.7	* 0.1	1.5	0.3	73.2	*	99.1	6.2	
	18.4	10.3	33.1	**	8.8	0	10.0	5.6	14.4	*	42.0	16.6	22.2	7.2	
Prelaying/laying Incubation Posthatching	15.8	8.0	44.7	62.1	5.6	0	8.9	6.9	17.1	17.0	—	—	7.9	6.0	
	18.1	*	5.8	23.6	*	0	4.7	3.4	6.7	23.5	—	—	39.3	61.2	
	27.8	18.6	32.2	**	8.4	0.7	11.2	5.9	16.4	*	53.4	—	11.6	13.0	
Posthatching	10.4	4.9	43.7	*	10.7	—	7.8	**	2.2	16.3	*	55.6	16.1	22.1	5.7

<sup>a</sup> Two swan pairs observed during prelaying/laying; five pairs observed during incubation; four pairs and broods observed during posthatching.

<sup>b</sup> Includes brooding after hatching.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

centage of the time budget and are included in Table 2 within the "other/unknown" category.

Potential predators of eggs, cygnets, or adult trumpeters were rarely seen at night. Coyotes (*Canis latrans*) were heard calling every evening near all territories, but were seen on only four occasions. A raccoon (*Procyon lotor*) and a striped skunk (*Mephitis mephitis*) each were observed once at night. The adult swans were aware of the presence of these animals, exhibiting alert postures and calling during two of the coyote encounters. During the raccoon encounter, the adults led their cygnets away from the shore to the center of the wetland. River otters (*Lutra canadensis*) were seen on two territories during the day, but not at night.

*Discussion.*—Night-vision scopes intensify available light, and birds that reflect more light are easier to observe. Large white swans were more obvious than darker-colored birds such as geese and ducks, but the latter were always viewable during average observation conditions. The most important feature of night-vision equipment is that it allows for direct, continuous observations. Indirect or discontinuous systems, such as electronic-monitoring devices or time-lapse cameras, are subject to malfunction and may lead to a misinterpretation of data. For example, Hampton (1981) used an electronic multiple-sensor system (Cooper and Afton 1981) to monitor nesting Trumpeter Swans in Idaho and concluded that incubating females took regular nightly recesses. We question the results of his study because incubation rhythms in his data are consistent with inaccuracies associated with battery drawdown in the monitoring system (Cooper and Afton 1981), and because nocturnal behavior was not directly observed and verified.

Our results demonstrate that staging and breeding Trumpeter Swans are active at night to varying degrees depending on the period of the breeding season. The nocturnal period is as important as the diurnal period to prelaying/laying females because individual birds spend considerably more time foraging than during the incubation and posthatching periods. Female geese and swans forage intensively during the prelaying phase of reproduction in order to build up nutrient and energy reserves for laying and incubation (Ryder 1970, Owen and Kear 1972, Inglis 1977, Fox and Madsen 1981, Bromley 1984, Gauthier and Tardif 1991). Trumpeter Swan females in Alaska follow this pattern (Grant 1991). During the incubation and posthatching periods, swans greatly curtailed nocturnal foraging, probably to prevent egg cooling during the lower nighttime temperatures and perhaps to discourage egg and cygnet predation. Female geese remain on the nest at night for the same reasons, even though the birds are energetically stressed (Aldrich and Raveling 1983, Thompson and Raveling 1987, Madsen et al. 1989).

Availability and quality of food resources on the breeding grounds are probably important determi-

nants of Trumpeter Swan breeding behavior (Henson and Cooper 1993). Cooper (1979) proposed that captive Trumpeter Swans are relatively independent of short-term weather variations during incubation due to their considerable body size and large eggs that cool slowly. However, wild Trumpeter Swan females in Alaska initiated significantly fewer incubation recesses early in the morning and late in the evening when temperatures were coolest, and the early and late recesses were shorter than midday recesses (Henson and Cooper 1993). These females also initiated fewer recesses in rainy weather than in clear or overcast weather. Female swans, like many other waterfowl, seem sensitive to environmental variables and minimize the cost of recesses by taking them in the warmest or driest parts of the day (see Afton and Paulus 1992). Hawkins (1986) documented similar patterns in Tundra Swans (*Cygnus columbianus columbianus*) nesting in Alaska.

The Idaho-Wyoming study area is located at greater than 2,000 m in elevation, and nocturnal temperatures were regularly below or near freezing during most of the incubation period. Trumpeter Swans in our study may avoid nocturnal recesses because the costs to eggs chilled by nighttime temperatures exceed energetic gains. Egg chilling, while not necessarily fatal to the embryos, could lengthen the incubation period and lower productivity (see Skutch 1976:202, Aldrich and Raveling 1983). Northern-breeding swans might have evolved higher rates of incubation constancy than temperate-breeding swans so as to minimize the length of the incubation period in areas with shorter breeding seasons (Kear 1972).

It is not known whether cygnets were directly influenced by nocturnal temperatures or if diel differences in cygnet behavior were due to issues related to age, such as foraging ability or experience or other environmental factors such as food availability (see Henson and Cooper 1993). Cygnets were brooded by females for longer periods at night, and cygnet nocturnal feeding bouts were shorter than diurnal bouts. Possibly, younger cygnets fed less at night than did older cygnets, but we were unable to detect feeding differences in our small sample. Owen and Kear (1972) proposed that young cygnets rely on visual cues for food selection in the days immediately after hatching, while older cygnets probably use touch to locate food items.

Predators probably are less important than ambient temperature in influencing nocturnal behavior of Trumpeter Swans. The large body size and protective behavior of adult swans discourages most avian and small mammalian predators (Banko 1960, Henson and Grant 1992). Incubating females never took nocturnal feeding recesses even though males were nearby and were available to defend eggs as they do during diurnal recesses (Henson and Grant 1991, Henson and Cooper 1992). We rarely observed nocturnal predators active near swan territories. Coyote predation on

nesting Trumpeter Swans has occurred in the study area (T. McEaney, Yellowstone National Park, pers. comm.), but island-nesting swans are less vulnerable to terrestrial predators than are geese and upland-nesting swans and ducks (Owen and Cadbury 1975, Henson and Grant 1992). In addition, potential avian predators such as corvids and non-owl raptors are mostly diurnal.

Our research demonstrates that behavioral studies of swans (and perhaps most other large birds) should include a study of nocturnal activities whenever possible. Nocturnal behavior patterns observed during our study were unexpected and provide evidence to better interpret diurnal swan behavior and energetics. Our results suggest that environmental variables influence nocturnal behavior. However, a larger sample of individual adult birds is needed to demonstrate a convincing relationship between ambient temperature and behavior patterns.

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#### LITERATURE CITED

- AFTON, A. D., AND S. L. PAULUS. 1992. Incubation and brood care. Pages 62–108 in *Ecology and management of breeding waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). Univ. Minnesota Press, Minneapolis.
- ALDRICH, T. W., AND D. G. RAVELING. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. *Auk* 100:670–679.
- ALTMANN, J. 1974. Observational study of behaviour: Sampling methods. *Behaviour* 49:227–267.
- BALDASSARRE, G. A., S. L. PAULUS, A. TAMISIER, AND R. D. TITMAN. 1988. Workshop summary: Techniques for timing activity of wintering waterfowl. Pages 181–190 in *Waterfowl in winter* (M. W. Weller, Ed.). Univ. Minnesota Press, Minneapolis.
- BANKO, W. E. 1960. The Trumpeter Swan: Its history, habits, and population in the United States. U.S. Fish Wildl. Ser., N. Am. Fauna 63.
- BROMLEY, R. G. 1984. The energetics of migration and reproduction of Dusky Canada Geese (*Branta canadensis occidentalis*). Ph.D. dissertation, Oregon State Univ., Corvallis.
- COOPER, J. A. 1979. Trumpeter Swan nesting behavior. *Wildfowl* 30:55–71.
- COOPER, J. A., AND A. D. AFTON. 1981. A multiple sensor system for monitoring avian nesting behavior. *Wilson Bull.* 93:325–333.
- EBBINGE, B., K. CANTERS, AND R. DRENT. 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl* 26:5–19.
- FOX, A. D., AND J. MADSEN. 1981. The pre-nesting behaviour of the Greenland Whitefronted Goose. *Wildfowl* 32:48–54.
- GAUTHIER, G., AND J. TARDIF. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. *Condor* 93:701–711.
- GRANT, T. A. 1991. Foraging ecology of Trumpeter Swans breeding on the Copper River Delta, Alaska. M.S. thesis, Univ. Minnesota, St. Paul.
- HAMPTON, P. D. 1981. The wintering and nesting behavior of the Trumpeter Swan. M.S. thesis, Univ. Montana, Missoula.
- HAWKINS, L. 1986. Nesting behaviour of male and female Whistling Swans and implications of male incubation. *Wildfowl* 37:5–27.
- HENSON, P., AND T. A. GRANT. 1991. The effects of human disturbance on Trumpeter Swan breeding behavior. *Wildl. Soc. Bull.* 19:248–257.
- HENSON, P., AND T. A. GRANT. 1992. Brown bear, *Ursus arctos middendorffi*, predation on a Trumpeter Swan, *Cygnus buccinator*, nest. *Can. Field-Nat.* 106:128–130.
- HENSON, P., AND J. A. COOPER. 1992. Division of labour in breeding Trumpeter Swans *Cygnus buccinator*. *Wildfowl* 43:40–48.
- HENSON, P., AND J. A. COOPER. 1993. Trumpeter Swan incubation in areas of differing food quality. *J. Wildl. Manage.* 57:709–716.
- INGLIS, I. R. 1977. The breeding behaviour of the Pink-footed Goose: Behavioural correlates of nesting success. *Anim. Behav.* 25:747–764.
- JORDE, D. G., AND R. B. OWEN. 1988. The need for nocturnal activity and energy budgets of waterfowl. Pages 169–180 in *Waterfowl in winter* (M. W. Weller, Ed.). Univ. Minnesota Press, Minneapolis.
- KEAR, J. 1972. Reproduction and family life. Pages 79–124 in *The swans* (P. Scott, Ed.). Houghton Mifflin Co., Boston.
- LAZARUS, J., AND I. R. INGLIS. 1978. The breeding behaviour of the Pink-footed Goose: Parental care and vigilant behaviour during the fledging period. *Behaviour* 65:62–88.
- LINSELL, S. E. 1969. Pre-dusk and nocturnal behav-

- our of Goldeneye, with notes on population composition. *Wildfowl* 20:75-77.
- MADSEN, J., T. BREGNBALLE, AND F. MEHLUM. 1989. Study of the breeding ecology and behaviour of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota*. *Polar Res.* 7:1-21.
- MAJ, M. B. 1983. Analysis of Trumpeter Swan habitat on the Targhee National Forest of Idaho and Wyoming. M.S. thesis, Montana State Univ., Bozeman.
- MCKELVEY, R. W., AND N. A. VERBEEK. 1988. Habitat use, behaviour, and management of Trumpeter Swans, *Cygnus buccinator*, wintering at Comox, British Columbia. *Can. Field-Nat.* 102:434-441.
- MOULTON, D. W., AND M. W. WELLER. 1984. Biology and conservation of the Laysan Duck (*Anas lay-sanensis*). *Condor* 86:105-117.
- NILSSON, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. *Oikos* 21:145-154.
- OWEN, M., AND C. J. CADBURY. 1975. The ecology and mortality of swans at Ouse Washes, England. *Wildfowl* 26:31-42.
- OWEN, M., AND J. KEAR. 1972. Food and feeding habits. Pages 58-77 in *The swans* (P. Scott, Ed.). Houghton Mifflin Co., Boston.
- PAULUS, S. L. 1984. Activity budgets of nonbreeding Gadwalls in Louisiana. *J. Wildl. Manage.* 48:371-380.
- PAULUS, S. L. 1988. Time-activity budgets of non-breeding Anatidae: A review. Pages 135-152 in *Waterfowl in winter* (M. W. Weller, Ed.). Univ. Minnesota Press, Minneapolis.
- PEDROLI, J. 1982. Activity and time-budget of Tufted Ducks on Swiss lakes during winter. *Wildfowl* 33:105-112.
- RAVELING, D., W. E. CREWS, AND W. D. KLIMSTRA. 1972. Activity patterns of Canada Geese during winter. *Wilson Bull.* 84:278-295.
- RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82:5-13.
- SHEA, R. E. 1979. The ecology of the Trumpeter Swan in Yellowstone National Park and vicinity. M.S. thesis, Univ. Montana, Missoula.
- SKUTCH, A. F. 1976. Parent birds and their young. Univ. Texas Press, Austin.
- SWANSON, G. A., AND A. B. SARGEANT. 1972. Observation of nighttime feeding behavior of ducks. *J. Wildl. Manage.* 36:959-961.
- TAMISIER, A. 1974. Etho-ecological studies of teal wintering in the Camargue (Rhône Delta, France). *Wildfowl* 25:123-133.
- TAMISIER, A. 1976. Diurnal activities of Green-winged Teal and Pintail wintering in Louisiana. *Wildfowl* 27:19-32.
- THOMPSON, S. C., AND D. G. RAVELING. 1987. Incubation behavior of Emperor Geese compared with other geese: Interactions of predation, body size, and energetics. *Auk* 104:707-716.
- YDENBERG, R. C., H. H. TH. PRINS, AND J. VAN DIJK. 1984. A lunar rhythm in the nocturnal foraging activities of wintering Barnacle Geese. *Wildfowl* 35:93-96.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

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## Patterns of Genetic Polymorphism in Five Species of Penguins

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Conservation programs benefit from increased knowledge of the basic biology and systematics of endangered species (Haig et al. 1990). This study focuses on relationships in the genus *Spheniscus*, which includes: Jackass Penguin (*S. demersus*), Galapagos Penguin (*S. mendiculus*), Humboldt Penguin (*S. humboldti*), and Magellanic Penguin (*S. magellanicus*). The first three taxa are considered threatened or endangered (U.S. Fish and Wildlife Service 1990, 1993). However, Jackass, Humboldt, and Magellanic pen-

guins are quite abundant in captivity, making this group well-suited for genetic and behavioral studies.

In addition to facilitating penguin research, captivity has led to mixed-species exhibits and interbreeding between *Spheniscus* species. Fertile hybrids between Jackass and Humboldt penguins and between Humboldt and Magellanic penguins have been reported in captivity (Conway 1965, Araya 1983). This raises questions concerning the species status of members of this group. The Galapagos and Jackass pen-