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Hybridization Between Barred and Spotted Owls

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Interspecific hybridization has been reported in at least 52 of 516 nonmarine bird species in North America (Johnsgard 1970, Mayr and Short 1970, Short 1965, 1972). It tends to occur infrequently, however, except where allopatric species are brought into contact by range expansions (Cade 1983). Groups in which interspecific hybridization is particularly common include warblers, grouse, and hummingbirds (Mayr and Short 1970, Oliphant 1991). Instances of interspecific hybridization in birds of prey are uncommon except in captivity (Newton 1979, Cade 1983, Oliphant 1991). In owls, interspecific hybridization appears to be rare. Johnsgard (1988) reported instances of hybridization between Eastern Screech-Owls (*Otus asio*) and Western Screech-Owls (*O. kennicottii*) in Texas, and Voous (1989) reported instances of hybridization between Whiskered Screech-Owls (*O. trichopsis*) and Western Screech-Owls in Arizona. Evidence of hybridization in the genus *Strix* has been limited to Ural Owls (*S. uralensis*) hybridizing with Tawny Owls (*S. aluco*) in captivity (Mikkola 1983). We present the first records of hybridization between the Northern Spotted Owl (*S. occidentalis caurina*) and Northern Barred Owl (*S. varia varia*), two species that are thought to be closely related and that have recently become sympatric (Grant 1966, Taylor and Forsman 1976, Hamer 1988).

Since at least the early 1950s, the Barred Owl has been expanding its range into western North America. In the process, it has invaded much of the historical range of the Spotted Owl (Grant 1966, Taylor and Forsman 1976, Hamer 1988). Barred Owls are now common in forested areas in southwestern British Columbia and northern Washington (Hamer 1988, Dunbar et al. 1991), and they are rapidly increasing in Oregon and northern California. Increasing sympatry between Barred and Spotted owls has led to speculation that the Northern Spotted Owl, which is listed as a threatened species (U.S. Fish and Wildlife Service 1990), may be further threatened by competition with the Barred Owl, as well as by habitat loss (Taylor and Forsman 1976, Dunbar et al. 1991). The possibility that sympatry might also result in hybridization between the two species has not been previously considered.

Records of hybrids.—Three adult Spotted Owl/Barred Owl hybrids, two in Washington and one in Oregon, were confirmed during 1989-1992, and one juvenile hybrid was produced by a female Barred Owl paired to a yearling male Spotted Owl in Oregon in 1992. All hybrids were identified by their unique plumage characteristics, vocalizations, and measurements. The first hybrid was an adult male seen on 23 March 1989 at Baker Lake in the Washington Cascades Range, 30 km south of the United States/Canadian border. This bird was fitted with a radio transmitter in 1989 and recorded in the same area in spring 1990, 1991, and 1992. Its nesting status was not determined, but it was always seen with a female Barred Owl. Both birds aggressively defended the territory in response to playback calls.

The second hybrid, an adult male located in the Klamath Mountains 29 km northeast of Medford, Oregon, in 1990 was paired with a female Barred Owl. This pair produced two young in 1990 and three young in 1991. In 1992 the Medford hybrid was displaced by a male Barred Owl. It was relocated in June 1992, 1 km from its previous nesting site and did not appear to be paired (James Harper pers. comm.). Another suspected hybrid (or possibly the same individual) was seen and heard in this area in 1987 (James Harper pers. comm.).

The third hybrid was an adult female observed several times in May 1991, 2 km south of Ozette Lake, Washington, near the northwestern tip of the Olympic Peninsula. When this bird was captured, we found that it had been banded as a juvenile in 1986, 277 km to the southeast in the Cascade Range of southern Washington. The original bander suspected that the bird may have been a hybrid, but was unsure because it was not fully feathered and because both parents were not observed (H. Allen pers. comm.). When located in 1991, the Ozette Lake female was paired with an adult male Spotted Owl. No young were observed, but the female had a brood patch that was regressing, which suggested that nesting may have been attempted. Both birds were observed together in 1992 when nesting was again attempted but failed for unknown reasons.

In addition to the three adult hybrids described above, a fourth hybrid from a pairing between a Barred Owl and Spotted Owl was confirmed in 1992 in Douglas County, Oregon, 8 km southeast of Canyonville. This pair consisted of a yearling male Spotted Owl and an adult female Barred Owl. They produced one young, which was first observed on 1 June 1992. The F_1 hybrid juvenile was fitted with a tail-mounted radio

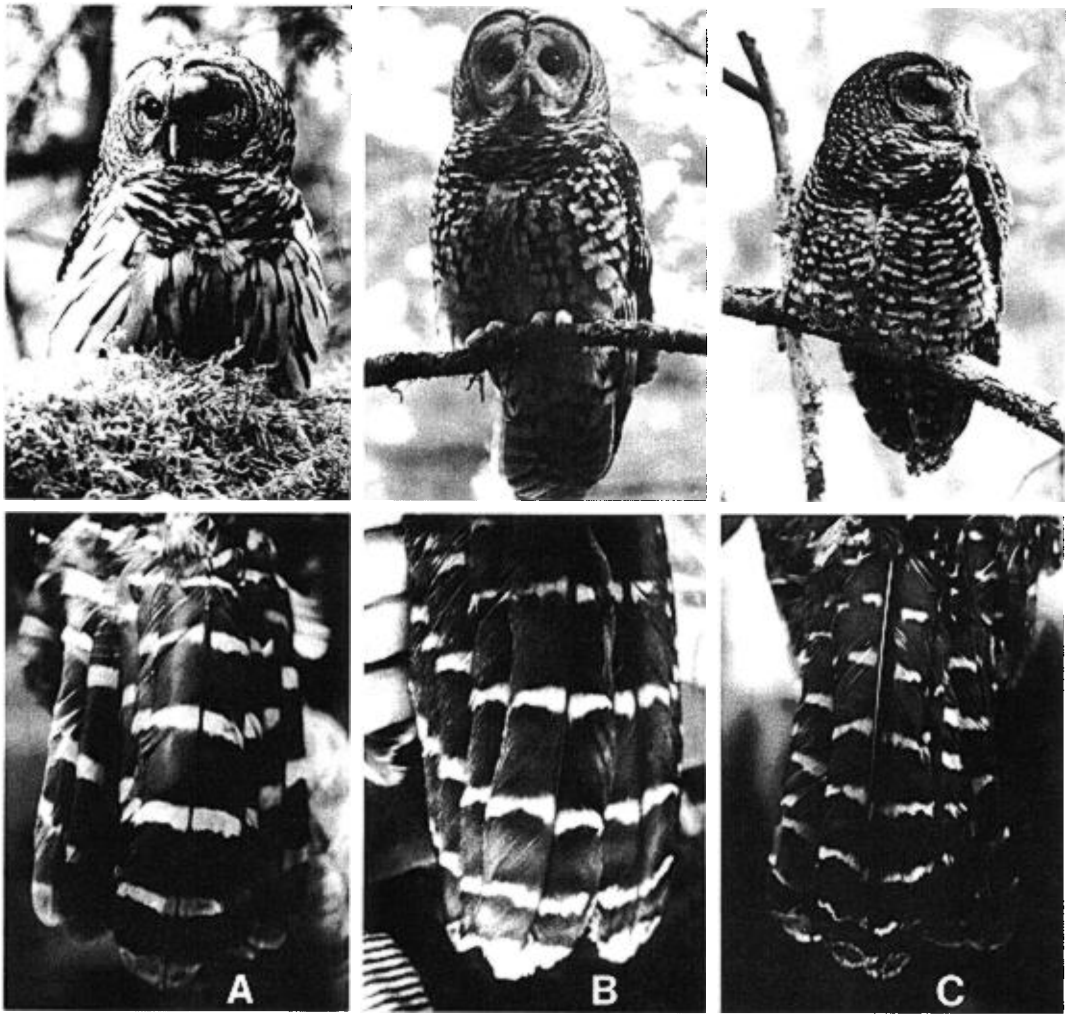

Fig. 1. Plumage characteristics and tail-barring pattern of: (A) Barred Owl; (B) Barred and Spotted owl hybrid; and (C) Spotted Owl.

transmitter and monitored periodically until the radio failed on 21 May 1993.

Description of hybrids.—All three adult hybrids and the F_1 juvenile hybrid had similar plumage characteristics that included attributes of both the Spotted Owl and Barred Owl (Fig. 1). The lower breast and abdomen were characterized by a checkerboard pattern of white patches separated by a network of broad, brown, vertical streaks and narrower horizontal brown bars (Fig. 1). The white patches were much more extensive than in the Spotted Owl, making the hybrid bird look much paler. The "collar" across the throat was barred horizontally, like the Barred Owl, and had large areas of white barring interspersed with the dark brown bars. The nape and top of the head of hybrids were covered by heavy white barring, as is typical of the Barred Owl (Fig. 1A). By comparison, the Spotted Owl has a pattern of irregular white spots on the nape and top of the head (Fig. 1C). The facial discs of hybrids were pale brownish gray, with distinct concentric rings around the eyes, much like the Barred Owl, except that the facial discs of the Barred Owl are gray (Fig. 1). The facial discs of the Spotted Owl are tawny brown, with less distinct concentric rings around the eyes. In the three adult hybrids, the beak was yellowish green, much like the Spotted Owl. The F_1 juvenile hybrid had a yellowish beak much like the Barred Owl.

The back and top of the wings of adult hybrids were a lighter brown than in the Spotted Owl, but still considerably darker than the pale brown of the Barred Owl. The white bars on the rectrices of hybrids were broad, spaced far apart, and tended to extend completely across the feathers, as is typical of the

TABLE 1. Measurements of three Barred and Spotted owl hybrids observed in Oregon and Washington, 1989–1991. Measurements ($\bar{x} \pm$ SE, with n in parentheses) from male and female Barred and Spotted owls provided for comparison.

Measurement[a]	Hybrid			Barred Owl		Spotted Owl	
	♂1	♂2	♀	♂	♀	♂	♀
Body mass	730	697	930	675.5 ± 11.37 (14)	802.0 ± 11.69 (16)	596.0 ± 7.91 (24)	691.7 ± 8.47 (24)
Wing chord	315	313	331	334.5 ± 5.53 (14)	357.1 ± 1.73 (18)	305.2 ± 1.30 (23)	311.8 ± 1.21 (21)
Tail length	211	214	212	235.1 ± 1.30 (15)	247.1 ± 2.93 (15)	192.1 ± 1.50 (20)	202.2 ± 1.47 (20)
Tail bar 1	10.8	—	9.2	15.15 ± 0.05 (2)	15.47 ± 0.80 (6)	8.45 ± 0.24 (30)	8.14 ± 0.20 (23)
Tail bar 2	15.3	—	11.9	18.38 ± 1.59 (2)	18.70 ± 0.76 (6)	11.68 ± 0.36 (30)	11.09 ± 0.64 (23)
Tail bar 3	19.9	—	15.2	22.10 ± 2.45 (2)	22.40 ± 0.79 (6)	14.86 ± 0.70 (25)	14.26 ± 0.73 (18)

[a] Mass in grams and other measurements in millimeters. Tail-bar measurements indicate closest distance between adjacent pairs of bottom three light-colored bars on central rectrices, beginning with terminal bar (bar 1). Measurements taken directly along feather shaft and averaged for both of innermost rectrices for each bar.

Barred Owl (Fig. 1). In the Spotted Owl, these bars are closer together, narrower, and often incomplete, extending only partway across the feathers (Fig. 1, Table 1).

One offspring of the hybrid/Barred Owl pair at the Medford site was observed in August 1990, after it had begun to develop its Basic I plumage. It had dark vertical bars on the lower breast and abdomen and was not easily distinguishable from a Barred Owl. Because its plumage was still not completely developed, however, we could not determine if it eventually developed any distinctive hybrid characteristics.

The body mass of adult hybrids was as great as or greater than average values for Barred Owls, and was at or above the upper limits of body mass for Spotted Owls (Table 1). The large body mass of hybrids was surprising because measurements of wing chord and tail length of hybrids were intermediate between mean values for Barred and Spotted owls (Table 1). We do not know whether hybrids typically weigh more than both of the parent species or this result was simply an artifact of small sample size. The spacing between the white bars on the rectrices of hybrids was greater than the average for Spotted Owls, and narrower than the average for Barred Owls (Table 1).

Hybrids were relatively tame and unafraid of humans, much like the Spotted Owl. By comparison, Barred Owls are more wary and typically depart when humans approach. The adult hybrids were so tame that we were able to capture two of them by grabbing them with our bare hands after luring them in with a live mouse decoy. This technique is commonly used for capturing Spotted Owls but is not usually effective for Barred Owls. We trapped the third adult hybrid using a noose pole (Forsman 1983), another technique that works well for Spotted Owls, but usually is not effective for Barred Owls.

The location call of the Spotted Owl is a four-note series of hoots, lasting 3 to 4 s (Fig. 2A; Forsman et al. 1984). The location call of the Barred Owl is a run-on series of eight notes lasting about 3.6 s and ending with a very distinctive, drawn-out "hooo-aww" note (Fig. 2B). Location calls of hybrids were strikingly different from either the Spotted or Barred owl (Figs. 2C, 2D, and 2E). The usual pattern was a series of five to six notes, ending in a note much like the "hooo-aww" note of the Barred Owl. When agitated, hybrids sometimes repeated this call two to five times in a closely spaced series. Sound frequency of location calls of hybrids was similar to both Spotted and Barred owls, with most of the energy concentrated at 0.5 kc/s (Figs. 2C, 2D, and 2E).

The contact call of the Spotted Owl and Barred Owl is a single, mellow whistle, ending with an upward inflection (Figs. 3A and 3B). The contact call of the hybrid male at Baker Lake was similar to both species, but appeared most similar to the Barred Owl, both in terms of duration and frequency (Fig. 3C).

Noticeably absent from the repertoire of the hybrids were calls that resembled the loud barking notes given by Spotted Owls. These calls, which Forsman et al. (1984) referred to as the "agitated location call" and "bark series call," are commonly heard from Spotted Owls, but have not been reported from Barred Owls.

Discussion.—The three adult hybrids and the juvenile F_1 hybrid looked like very large, very pale Spotted Owls, with heavy white barring on the head, Barred Owl-like facial features and tail bars, and a network of brown streaks and bars on the breast that created a checkerboard pattern of large white patches. Based on the similarity of their plumage, we believe that these birds were all F_1 crosses between Barred and Spotted owls.

Offspring produced by backcrosses between F_1 hybrids and Barred Owls are difficult to identify as hybrids, as evidenced by the offspring of the male hybrid and female Barred Owl at Medford. We have yet to confirm a backcross between an F_1 hybrid and a Spotted Owl, so do not know what offspring of such a mating would look like. Anyone working with either Spotted Owls or Barred Owls should pay particular attention to minor differences in vocalizations, behavior, and plumage, because hybrids beyond the first generation may be difficult to identify. Ulti-

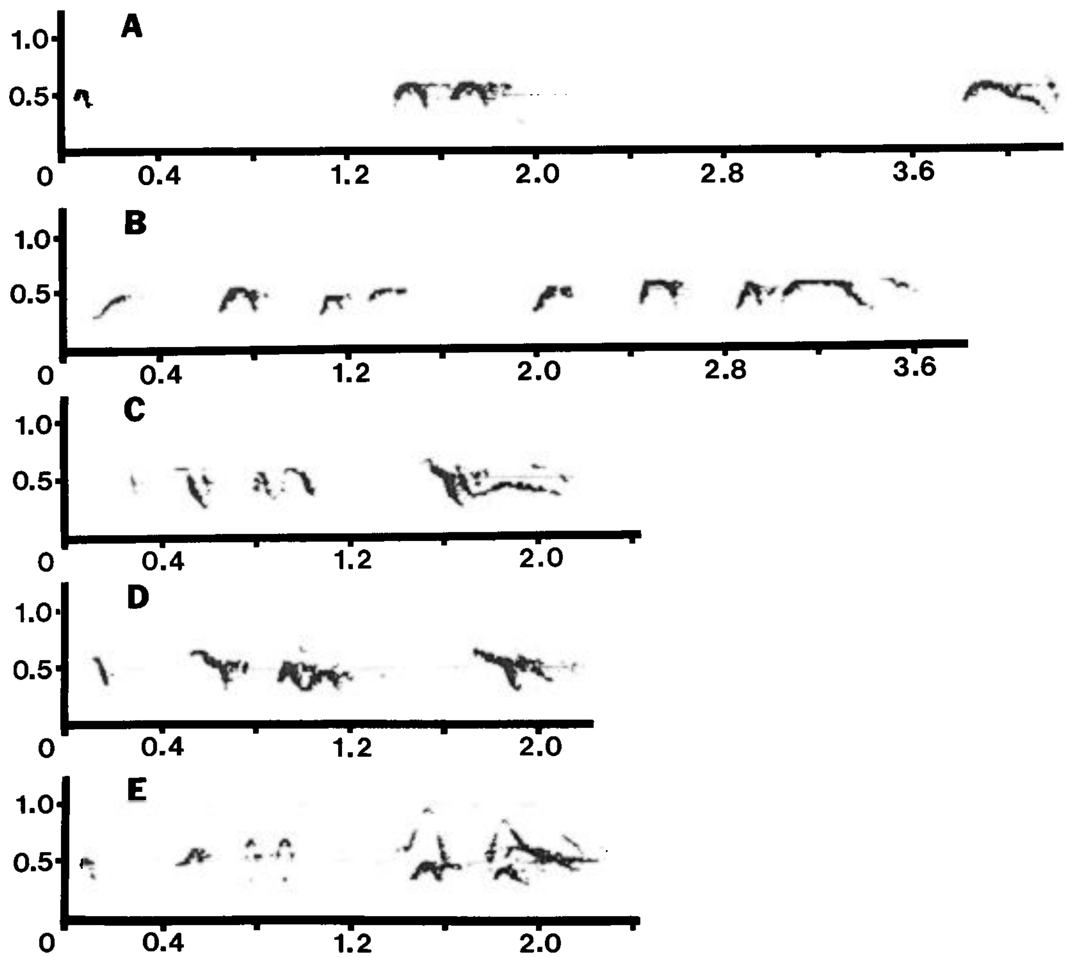

Fig. 2. Sonagrams of typical location calls of: (A) male Spotted Owl; (B) male Barred Owl; (C) 1987 suspected male Barred and Spotted owl hybrid at Medford; (D) 1990 Medford male Barred and Spotted owl hybrid; and (E) 1990 Baker Lake male Barred and Spotted owl hybrid. *Y*-axis in kilocycles per second (kc/s), and *X*-axis in seconds (s).

mately, genetic comparisons of blood or other tissues may be the only way to identify hybrids beyond the first generation.

During the last 20 years, numerous surveys for Spotted Owls have been conducted in Oregon, Washington, California, and British Columbia. Thousands of pairs have been located, and several thousand birds have been banded. The fact that only four F_1 hybrids (three adults and one young) have been detected during this effort suggests that hybridization is relatively rare. Hybridization may have been overlooked however, because in the past, where field workers heard Barred and Spotted owls in the same areas, it was assumed that the owls were members of separate pairs. In the future, observers need to be careful to document pair relations when sympatry occurs.

Hybridization between Barred and Spotted owls, and successful backcrossing by the F_1 hybrids, indicates that the designation of the Barred Owl and Spotted Owl as a superspecies (Mayr and Short 1970) may be appropriate. However, the degree to which these species are related should be evaluated with detailed genetic comparisons before any definitive conclusions are drawn.

We can only speculate about the eventual outcome of hybridization between the Barred Owl and Spotted Owl, a process that may take many decades to unfold. The continued range expansion of the Barred Owl may result in the proliferation of hybrid phenotypes, competition with the Spotted Owl, and the eventual exclusion or elimination of the Spotted Owl from portions of its range. A similar scenario has been reported for the Blue-winged Warbler (*Vermivora pinus*) and Golden-winged Warbler (*V. chrysoptera*) in the

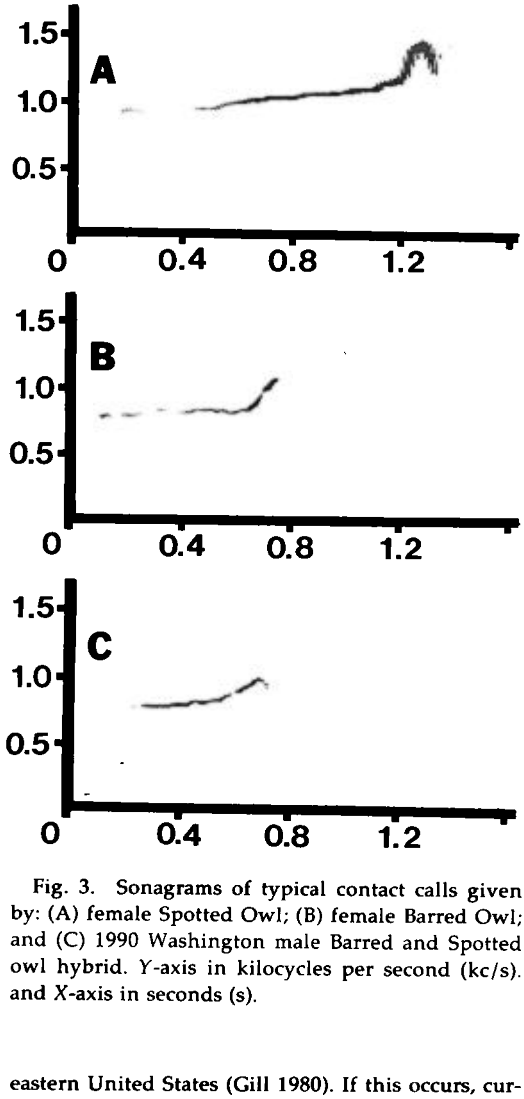

Fig. 3. Sonagrams of typical contact calls given by: (A) female Spotted Owl; (B) female Barred Owl; and (C) 1990 Washington male Barred and Spotted owl hybrid. Y-axis in kilocycles per second (kc/s). and X-axis in seconds (s).

eastern United States (Gill 1980). If this occurs, current habitat- and population-management strategies for the Spotted Owl would have to be reassessed. Another possibility is that the isolating mechanisms that separate the Spotted Owl and Barred Owl will be effective enough to maintain hybridization at a very low incidence, such that both species will continue to exist within a zone of overlap and hybridization (Short 1972). We believe the latter scenario is more likely because the relative infrequency of hybridization between Barred and Spotted owls indicates that isolating mechanisms are relatively effective. The early documentation of hybridization between species in recent secondary contact provides a unique opportunity to document the processes of hybridization and speciation from their inception.

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Daily Body-mass Loss and Nitrogen Excretion During Molting Fast of Macaroni Penguins

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Little is known about the dynamics of protein and energy requirements during avian molt (Murphy and King 1991). In passerine birds, changes in protein requirements appear to resemble those in energy expenditure (Murphy and King 1991). However, no clear relationships have emerged due to the complexity of the metabolic processes. In most species, plumage renewal is a gradual, long-term process. This, combined with the fact that birds feed while molting, makes quantifying the allocation of exogenous and endogenous nutrients to keratin synthesis and energy expenditure difficult.

Unlike other bird species, penguins renew all their feathers over a protracted period (two to five weeks) during which they fast completely (Adams and Brown 1990, Groscolas and Cherel 1992). Thus, penguins rely entirely on their endogenous nutrient stores for both feather synthesis and energy expenditure during molt, and molt is preceded by the buildup of protein and lipid reserves (Cherel et al. 1993). To investigate the dynamics of protein and energy requirements during avian molt, we measured daily changes in body-mass loss and nitrogen excretion in Macaroni Penguins (*Eudyptes chrysolophus*) during their molting fast. In molting King Penguins (*Aptenodytes patagenicus*), the daily loss in body mass follows a pattern similar to that of energy expenditure (Adams and Brown 1990, Groscolas and Cherel 1992) and, therefore, it is a relatively simple way to get a first insight into the energy expenditure of molting penguins.

Methods.—Our study was carried out at the subantarctic Possession Island, Crozet Archipelago (46°25'S, 51°45'E). Six adult Macaroni Penguins were captured when first sighted ashore, at the beginning of their molting fast, in March 1987. Each bird was weighed (accuracy ± 10 g) at capture and daily thereafter. Four penguins were kept outdoors in a fenced area. The other two were placed alone in wire-bottomed metabolism cages in a room at external temperature. Guano was collected every day following the procedure of Robin et al. (1987). Fallen old feathers have been carefully discarded from guano. Total nitrogen in the guano was determined by the method of Kjeldahl, using selenium as catalyzer. Values are means and standard errors. Peritz' F-test (Harper 1984) was used for statistical comparisons.

Results and Discussion.—The mean body mass of the six Macaroni Penguins was 5.76 $\pm$ SD of 0.15 kg at capture. After 31.5 $\pm$ 1.4 days of fasting, their mass was 2.56 $\pm$ 0.07 kg, which corresponds to a 55.6 $\pm$ 0.8% decrease in mass. In birds and mammals, changes in the specific daily body mass loss ($dm/m \cdot dt$) allow the determination of three different phases during long-term fasting (Cherel et al. 1988b). During the first days of the fast, in Macaroni Penguins, $dm/m \cdot dt$ decreased ($P < 0.01$) from 28.5 $\pm$ 1.5 (day 1) to 19.7 $\pm$ 1.4 $g \cdot kg^{-1} \cdot day^{-1}$ (day 4). However, during the last days, $dm/m \cdot dt$ increased ($P < 0.05$) from 23.0 $\pm$ 3.0 (day 30) to 34.1 $\pm$ 3.9 $g \cdot kg^{-1} \cdot day^{-1}$ (day 32). These initial and final variations in $dm/m \cdot dt$ characterize, respectively, phases I and III of fasting previously described in molting and nonmolting King Penguins and Emperor Penguins (*A. forsteri*; Groscolas 1990, Groscolas and Cherel 1992).

Phase I of fasting is adaptive because it is marked by a decrease in basal metabolic rate, mobilization of fat stores and a reduction in protein use (Cherel et al. 1988b). In this study, no large decreases in daily body-mass loss and nitrogen excretion occurred during the first days after Macaroni Penguins came ashore (Fig. 1). The main reason for this is probably that

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