WHY DO *APTENODYTES* PENGUINS HAVE HIGH DIVORCE RATES?

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ABSTRACT.—In long-lived birds, monogamy is thought to enable breeders to retain the same mate from year to year, but exceptions occur. For example, King Penguins (*Aptenodytes patagonicus*) and Emperor Penguins (*A. forsteri*) have much lower mate fidelity than do smaller species of penguins, despite their high rates of survival. Recently, Olsson (1998) suggested that divorce in King Penguins could be adaptive. Although Olsson was the first to propose an adaptive function for divorce in this species, he was unable to assess the relationships among individual quality, date of arrival, mate choice, and breeding success. Accordingly, we studied King Penguins and Emperor Penguins to further examine the determinants and consequences of divorce. Mate retention was not affected by breeding performance in the previous year or by experience, and neither mate retention nor divorce had significant consequences on chick production the following year. King Penguins were more likely to divorce as arrival asynchrony of previous partners increased. In Emperor Penguins, this tendency to divorce occurred only when females returned earlier than their previous mates. Most Emperor Penguin pairs formed within 24 hours after the arrival of males, which were outnumbered by females. King Penguins that had nested successfully in their next to last attempt were favored as mates for ones that had been unsuccessful, and individuals of both species probably chose the best mates available. Most of our results for King Penguins and Emperor Penguins supported Olsson's (1998) conclusions in that divorce appears to be adaptive. Mate retention in the absence of a true nesting site (neither species builds a nest) would be maladaptive for these species, which face strong time constraints for breeding. Therefore, divorce occurs because costs of mate retention are high. *Aptenodytes* penguins appear to have adopted an optimal divorce strategy in order to adapt to their long breeding cycle in a demanding environment. *Received 27 June 1998, accepted 30 October 1998.*

SOCIAL MONOGAMY is the predominant mating system among birds (Lack 1968), and many long-lived species have a long reproductive life span (Stearns 1992). High survival may enable monogamous species to retain the same mate between successive breeding attempts more frequently than do species with higher mortality (Rowley 1983). In addition, breeding success often is enhanced by mate retention (e.g. Rowley 1983, Ens et al. 1996).

High survival rates and long reproductive life spans are common in seabirds (Ricklefs 1990), but mate fidelity varies among groups. For example, albatrosses are very faithful to their partners (Rowley 1983, Warham 1990), whereas frigatebirds regularly divorce (see Black 1996) between successive breeding attempts (Nelson 1976). This variability also occurs within the same family, as is the case for penguins (Williams 1996). The genus *Aptenodytes* is unique in that adults do not build a nest, incubating their single egg and brooding

their chick on top of their feet. Only two species occur in this genus, the King Penguin (*Aptenodytes patagonicus*) and the Emperor Penguin (*A. forsteri*). Being the largest species of penguins, they have a long breeding cycle, part of which takes place during the austral winter (Stonehouse 1953, 1960). Consequently, they must optimize their reproductive output during severe conditions that involve a decline in food availability and a four-month winter fast for chicks of the subantarctic King Penguin (Stonehouse 1960, Weimerskirch et al. 1992), and low temperatures and ice for the antarctic Emperor Penguin (Stonehouse 1953). In addition, both species face strong time constraints for breeding. Thus, laying after the end of January at Iles Crozet or after 1 January on South Georgia Island invariably results in breeding failure in King Penguins (Weimerskirch et al. 1992, Jouventin and Lagarde 1995, Olsson 1996) because late-hatched chicks have not been able to store sufficient fat reserves before the austral winter (Stonehouse 1960, Van Heezik et al. 1994, Jouventin and Lagarde 1995). In the more synchro-

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nously breeding Emperor Penguin (Stonehouse 1953, 1960; Isenmann 1971; Weimerskirch et al. 1992), only the earliest-hatched chicks (i.e. before 10 August; Isenmann 1971) are able to depart to sea when the ice breaks in December, having completed their molt but attaining only 50% of adult body mass (Isenmann 1971).

Aptenodytes penguins are long lived, with a mean annual survival rate of 0.91 to 0.95 (Jouventin and Weimerskirch 1991, Weimerskirch et al. 1992). Yet, they show low mate fidelity between years (15% in Emperor Penguin [Isenmann 1971, Jouventin 1971]; 19 to 29% in King Penguin [Barrat 1976, Olsson 1998]) compared with other penguins ($\bar{x}$ = 84%; Williams 1996). For divorce to be adaptive, individuals that divorce should obtain some benefit; i.e. it would be "optimal" for an individual to divorce if its reproductive success from breeding with a previous partner in the next year is lower than its average future success (i.e. the average for all future breeding attempts until the individual dies; McNamara and Forslund 1996).

Several hypotheses have been put forward to explain divorce in birds (e.g. Ens et al. 1993, Choudhury 1995), including penguins (Williams 1996). The "incompatibility" hypothesis predicts that pairs having low breeding success are more likely to divorce, and that each of the previous partners should be more successful with its new mate (Coulson 1966, Rowley 1983). In species with part-time pair bonds (i.e. during part of the year only), the main reason for pairs to split might be asynchronous returns by previous mates (Coulson 1972, Boekelheide and Ainley 1989, Davis and Speirs 1990). In his study of King Penguins, Barrat (1976) also hypothesized that divorce is caused by the asynchronous return of previous partners to the colony. However, his assumption was based on a small sample (three pairs), and his study was conducted during only one breeding season. Recently, Olsson (1998) showed that divorce rates in King Penguins from South Georgia Island increased as the previous mates returned more asynchronously to the colony, confirming Barrat's (1976) hypothesis. He also showed that King Penguins came ashore at the onset of the breeding cycle with only half of their body reserves. Because they fast when on land, their fat stores were close to exhaustion at the end of their first stay in the colony. Accordingly, Olsson (1998) pro-

posed the "expensive fat-storing" hypothesis, suggesting that individuals would face a trade-off between the costs of divorce and the costs of building up reserves while waiting for their previous partners so that mate retention would occur. Although Olsson believed that divorce was adaptive in King Penguins, his study still needed to be supplemented in some respects. In particular, he did not evaluate accurately the eventual benefits (in terms of offspring production) of extensive divorce, and he did not analyze the relationships among individual quality, date of arrival, mate choice, and breeding success. Despite a lack of data on Emperor Penguins, Olsson (1998) also suspected that his hypotheses were relevant for this species; like the King Penguin, Emperor Penguins have part-time pair bonds, and fat reserves play a major role during courtship and incubation (Prévost 1961, Isenmann 1971). Here we provide results from our long-term study of King Penguins, supplemented with data from Emperor Penguins, that enabled us to further assess the adaptive value of divorce in these species.

STUDY AREA AND METHODS

From September 1990 to March 1994, we conducted a demographic study of King Penguins in a small colony (750 pairs) on Possession Island, Crozet Archipelago (46°25'S, 51°45'E). We attached flipper bands to 989 birds and checked for their presence every other day. To assess the influence of previous reproductive success on divorce, we considered pairs to be successful if at least one mate was seen feeding a chick after September, or was molting after November. If the egg did not hatch, or if one of the parents was molting before December or displaying in early December, the pair was assumed to have failed (Jouventin and Lagarde 1995). At best, King Penguins can breed successfully every other year (Weimerskirch et al. 1992, Olsson 1996). Therefore, individual quality at the onset of breeding cycle n was defined from the reproductive performance at breeding cycle $n - 2$ (Olsson 1996).

Data on Emperor Penguins were from studies conducted in 1968 by P. Isenmann (pers. comm.) and in 1969 by P. Jouventin. Field work was carried out at a colony (12,500 pairs) on Pointe Géologie, Terre Adélie, Antarctica (66°40'S, 140°E), where flipper tags were attached to 855 individuals between 1965 and 1967. From arrival until laying, daily observations were performed on banded birds that were known to have bred in 1967 and 1968. Thus, dates of arrival at the colony (in 1968 and 1969) and pair formation (in

1969) were known accurately for each individual. Pairs in which one mate was seen feeding a chick after 15 November were considered successful.

For both species, observations lasted for half a day so that the same individual could be observed several times while performing different activities. Sex was determined from measurements and behavior (Prévost 1961, Jouventin 1982) whenever possible. Individuals that lost their band in the course of the study, or that paired with an unbanded partner while their previous (banded) partner was not observed (the rate of band loss is 22.3% in the first year after banding for King Penguins; Weimerskirch et al. 1992), were excluded from our data set. To assess the effect of the asynchrony of returns of previous partners on mate fidelity in King Penguins, we controlled for the effects of previous breeding performance (successful vs. unsuccessful) and breeding experience, because these parameters are known to influence mate retention in a number of species (Greenwood and Harvey 1982, Coulson and Thomas 1983).

We performed stepwise logistic regressions using PROC CATMOD (maximum-likelihood analysis) of SAS (1988). Only the best-fitting (i.e. most parsimonious) models are presented in the Results. It was not possible to control for previous breeding performance in Emperor Penguins because we did not know whether 1967 breeding pairs were successful or failed prior to divorce or remating. Breeding success was known for some pairs that bred in 1968, but we did not take it into account because our sample size was too small for reliable analyses. When controlling for breeding experience, we considered only the known experience of individuals (i.e. the number of breeding attempts since the beginning of our study, not the number of breeding attempts performed by an individual since it recruited into the breeding population). If the same bird was observed during several consecutive years, we avoided pseudoreplication by calculating the mean value for each parameter before conducting our analyses. G-tests were performed using Williams' correction. All tests were considered significant at $P < 0.05$.

RESULTS

Pair-bond duration and mate fidelity.—The duration of pair bonds in King Penguins never exceeded two successive years, and the probability of divorce was 78% ($n = 76$ pair years). Mate fidelity (22%) tended to be higher than that found in two consecutive years for Emperor Penguins (15%) by Isenmann (1971; 41 pairs) and Jouventin (this study; 21 pairs), although the difference was not significant ($G = 1.37$, df $= 1, P > 0.2$). Pair bonds lasted up to four years in Emperor Penguins.
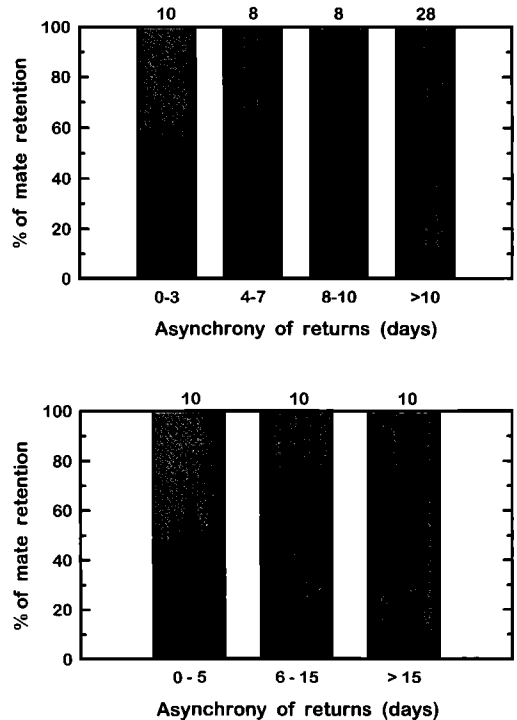

FIG. 1. Mate retention and asynchrony of return of partners from the previous year in King Penguins (top) and Emperor Penguins (bottom). Successful and unsuccessful pairs were pooled. Black bars = mate-fidelity rates, gray bars = divorce rates; sample sizes indicated above bars.

Potential factors in divorce.—Among King Penguin pairs for which return dates were known for both mates, mates of the 39 pairs that divorced were more asynchronous in returning to the colony ($\bar{x} = 15.3 \pm$ SD of 9.8 days) than were those of the 16 pairs that reunited ($\bar{x} = 5.9 \pm 5.0$ days). Likewise, return asynchrony of previous partners was significantly higher in unsuccessful pairs ($\bar{x} = 13.6 \pm 9.8$ days, $n = 48$) than in successful pairs ($\bar{x} = 5.3 \pm 6.0$ days, $n = 6$; Kolmogorov-Smirnov test, $D = 0.60, P = 0.04$). However, preliminary models given by the CATMOD procedure failed to find a significant effect of previous reproductive performance and breeding experience of pairs on mate retention, which decreased significantly as the second partner returned to the colony later (best-fitting model; asynchrony, $\chi^2 = 9.06$, df $= 1, P = 0.026, n = 54$ pairs; see Fig. 1). Among pairs that divorced, asynchrony of previous partners was similar regardless of which
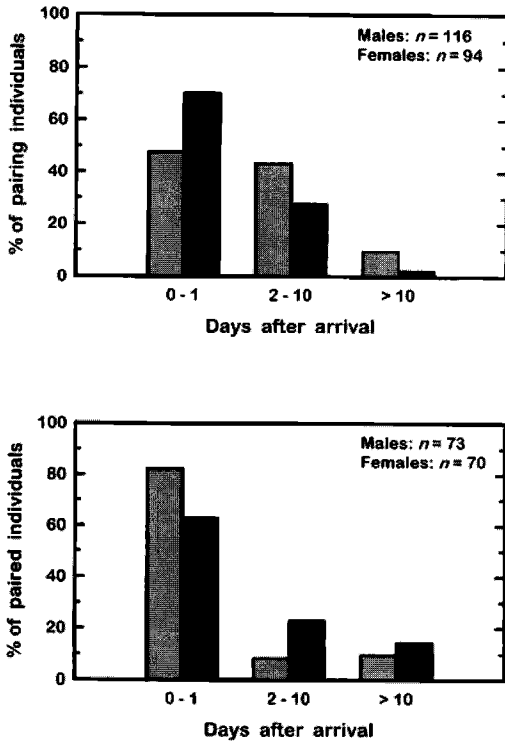
FIG. 2. Time elapsed between arrival and courting in King Penguins (top) and between arrival and pairing in Emperor Penguins (bottom). Gray bars = males, black bars = females.

sex returned the earliest. Independent of fidelity, females began courting significantly faster after returning to the colony ($\bar{x} = 1.9 \pm 4.3$ days, $n = 94$) than did males ($\bar{x} = 4.0 \pm 6.3$ days, $n = 116$; $D = 0.25$, $P = 0.003$). Consequently, 63% of females, but only 38% of males, were seen courting potential partners during the 24 hours after their arrival (Fig. 2). In divorced pairs, the partner that arrived earliest was already performing courtship display when its previous mate returned in 37 cases, and was still alone in one case.

In Emperor Penguins ($n = 26$ pairs), neither asynchrony of previous partners, nor the sex of the partner that returned first, nor experience of breeding pairs (one breeding attempt vs. more than one attempt) affected the probability of divorce. Yet, the latter factor tended to depend on the interaction between the former two factors, although not significantly so (asynchrony, $\chi^2 = 0.51$, df = 1, $P = 0.47$; sex, $\chi^2 = 2.20$, df = 1, $P = 0.14$; experience, $\chi^2 = 1.90$, df = 1, $P = 0.17$; asynchrony × sex, $\chi^2 = 2.74$, df

= 1, $P = 0.097$; see Fig. 1). Among pairs in which the female returned to the colony earlier than the male ($n = 18$), divorce tended to occur more frequently as asynchrony increased, but this tendency was not significant (asynchrony, $\chi^2 = 3.33$, df = 1, $P = 0.068$; experience, $\chi^2 = 0.22$, df = 1, $P = 0.63$). Female Emperor Penguins returned earlier than males both in 1968 and 1969, the difference being significant in 1969 (Wilcoxon's rank-sum test, $z = 2.15$, $n_1 = 92$, $n_2 = 86$, $P = 0.031$). Females also spent significantly more time between returning and pairing ($\bar{x} = 4.4 \pm 7.3$ days, $n = 70$) in 1969 than did males ($\bar{x} = 1.9 \pm 5.0$ days, $n = 73$; Kolmogorov-Smirnov test, $D = 0.26$, $P = 0.013$). Consequently, 82% of males and 56% of females paired within 24 hours after their arrival (Fig. 2). For divorced pairs in which pairing date of the first-arrived mate was known, the second partner returned to the colony after its previous mate was paired in 7 cases and while its previous mate was unpaired in 12 cases.

Data on breeding success in the previous year were available for 74 pairs of King Penguins. For Emperor Penguins, data on breeding attempts in the previous year were available for 36 pairs, but we knew the outcome of those attempts for only six pairs. Considering reproductive performance per capita (i.e. over the total number of individuals or pairs studied), in both species pairs that divorced produced as many chicks as those that reunited in the next year (data for King Penguins; divorce, $\chi^2 = 0.06$, df = 1, $P = 0.8$, experience, $\chi^2 = 0.01$, df = 1, $P = 0.91$, $n = 74$). However, high-quality King Penguins (i.e. successful breeders in next to last breeding cycle) tended to divorce less often than poor-quality ones, although the difference was not significant (quality, $\chi^2 = 3.12$, df = 1, $P = 0.077$; experience, $\chi^2 = 0.63$, df = 1, $P = 0.43$, $n = 69$).

Olsson (1995) found a slight surplus of males in the King Penguin colony he studied on South Georgia, although he did not assess its importance. In our Iles Crozet colony, 428 of the 989 banded King Penguins could be sexed, yielding a ratio of 1.53 males per female (259 males, 169 females). Yet, males are easier to identify than females because they perform displays more often. Consequently, we may have overestimated the proportion of males in the King Penguin population. In the Emperor Penguin, Isenmann (1971) and Jouventin (1971) showed that fe-

males outnumbered males by about 10% at Pointe Géologie. For both species, reproductive performance in the year before divorcing or re-uniting did not differ significantly from that in the year following a divorce or remating with a previous partner.

Mate retention vs. divorce: Costs and benefits.— Retaining one's partner or divorcing had no significant effect on reproductive performance in the next year in King Penguins, even if we controlled for previous breeding experience. In Emperor Penguins, divorced individuals tend-ed to produce more offspring ($\bar{x} = 0.47$ chicks) than those that remated ($\bar{x} = 0.17$ chicks) with their previous partners, but the difference was not significant (preliminary model; experience, $P = 0.14$; best-fitting model; mate retention, $\chi^2 = 3.28$, df = 1, $P = 0.07$; sex, $\chi^2 = 0.47$, df = 1, $P = 0.49$, $n = 63$). In neither species did date of arrival (earlier or later than previous partner) or sex have a significant effect on breeding sta-tus (breeder or nonbreeder) during the year fol-lowing a divorce.

Individual quality and mate choice.—In King Penguins, high-quality individuals (see above) tended to return to the colony earlier than birds that had failed, but the difference was not sig-nificant (Wilcoxon's rank-sum test, $z = 1.84$, $n_1 = 18$, $n_2 = 96$, $P = 0.065$). The probability of successfully raising a chick tended to be higher in pairs with at least one high-quality mate (20%, $n = 15$) than in pairs formed by two low-quality mates (0%, $n = 18$), but again, the dif-ference was not quite significant (Fisher's exact test, $P = 0.08$). Because high-quality individu-als appeared to be at a reproductive advantage, we examined whether mate quality was an im-portant criterion in mate choice. Low-quality individuals were significantly more likely to obtain a high-quality partner than were high-quality ones, and the interaction between in-dividual quality and return date also had a sig-nificant effect on the quality of the mate chosen (individual quality, $\chi^2 = 4.48$, df = 1, $P = 0.034$, date × individual quality, $\chi^2 = 5.54$, df = 1, $P = 0.018$, $n = 54$). Preliminary models failed to reveal a significant effect of experience. Mate quality did not seem to depend on return date in high-quality individuals (sex, $\chi^2 = 0.13$, df = 1, $P = 0.72$; date, $\chi^2 = 0.74$, df = 1, $P = 0.39$, $n = 10$). In contrast, low-quality individuals (i.e. failed breeders two cycles earlier) were more likely to obtain a low-quality partner when

they returned to the colony later (date of return, $\chi^2 = 4.97$, df = 1, $P = 0.026$, $n = 44$). We knew the quality of the new and the former mates for five individuals that divorced, and they were similar in all cases. For Emperor Penguins, the very small number of individuals for which re-productive performance was known during the previous breeding season precluded the analy-ses that we performed for King Penguins.

DISCUSSION

Factors in divorce: "Asynchrony of return" and "fat-storage" hypotheses.—Mate retention in our King Penguin colony occurred more frequently if both partners of the previous year returned synchronously at the start of the breeding sea-son, confirming Barrat's (1976) hypothesis for King Penguins in another colony on Iles Crozet and Olsson's (1998) results from South Georgia Island. In Emperor Penguins, asynchrony also might play a role, but only in those pairs in which females (i.e. the most represented sex) return the earliest. However, and like in Ols-son's (1998) King Penguin colony, the incidence of divorce was high (50% in Crozet King Pen-guins and 60% in Emperor Penguins; Fig. 1) even when asynchrony was low, confirming that this factor alone was not sufficient to ex-plain high divorce rates in *Aptenodytes* pen-guins.

Olsson (1998) also suggested that mate shift-ing in King Penguins depended on the amount of fat stored. According to the "expensive fat-storing" hypothesis, attaining fat reserves be-fore mating is costly owing to decreased ma-neuverability in the water and decreased fight-ing ability, and because storing fat to ensure re-mating with one's partner from the previous year can imply late breeding. Thus, individuals would face a tradeoff between the costs of di-vorce and those of mate retention. In Emperor Penguins, females return to the colony in April with lower fat reserves than do males (Prévost 1961). Once ashore, they fast until egg laying, which occurs in May. Thereafter, they under-take a long foraging trip at sea to replenish their body reserves. Meanwhile, males take charge of incubation (Prévost 1961). Their fast will end at the beginning of chick rearing, when females relieve them (Isenmann 1971). We therefore suggest that female Emperor Pen-guins face a tradeoff between replenishing

their body reserves before fasting during court-ship, and the potential costs of divorce and late breeding, or of not breeding at all if they cannot find a male. Storing and carrying fat also is costly for adult males, which have lower sur-vival rates in this species (Jouventin and Wei-merskirch 1991), partly because they are more vulnerable to predation at sea than are females (Jouventin 1974). While at sea during this pe-riod, their maneuverability is decreased, which also is consistent with the "expensive fat-stor-ing" hypothesis. In both species, laying (and hence, mating) as early as possible should en-able the female to limit the duration of her for-aging trip at sea before she relieves her incu-bating mate. Simultaneously, the probability that males would exhaust their fat reserves and abandon their eggs should decrease. Individu-als of both sexes should obtain a mate before their body reserves are reduced to a critical threshold; beyond this threshold, a breeding at-tempt almost invariably would result in failure.

Factors in divorce: Sex ratio.—Female Emperor Penguins, which seem to return earlier and are slightly more numerous than males, tend to monopolize each solitary male upon its arrival at the colony (Isenmann 1971, Jouventin 1971) so that pair formation occurs almost immedi-ately after males have arrived (Isenmann 1971, this study). As a result, the earlier a female re-turns at the onset of the breeding cycle (1) the higher the probability she will get a mate (Is-enmann 1971), and (2) the lower the probability that her previous mate will already be paired with another female. Consequently, the unbal-anced sex ratio in Emperor Penguins, com-bined with the body-reserve problem noted above (plus the physiological synchrony of in-dividuals and the advantage of breeding as ear-ly as possible), may be a factor in divorce in this species. Monopolizing partners has not been recorded in King Penguins. Moreover, Yellow-eyed Penguins (*Megadyptes antipodes*) and Little Penguins (*Eudyptula minor*) have high mate fi-delity (82%; Richdale 1947, Reilly and Cullen 1981, Dann and Cullen 1990) despite biased sex ratios. Therefore, a biased sex ratio is unlikely to be a general factor in divorce among sphen-isciforms. The Emperor Penguin seems to be an exception, but only because the different phas-es of its breeding cycle occur more synchro-nously than in King Penguins, and Emperor Penguins are under much more severe time

constraints than the latter two species that live at lower latitudes (Marchant and Higgins 1990).

Absence of a nest site.—Penguins generally live in huge colonies (Marchant and Higgins 1990). Locating one's previous partner among several thousand individuals apparently is much easier for penguins that build nests or dig burrows (Jouventin 1982), and these territorial species tend to exhibit strong nest-site tenacity (60 to 98% for nine species) and high mate fi-delity (up to 97%; Williams 1996). Nonetheless, Williams (1996) found no significant correla-tion between mate retention and nest-site fi-delity among 14 species of penguins. In addi-tion, if individuals divorce simply because they are unable to locate their previous partner, then divorce should occur less frequently in the smallest colonies. Yet, Barrat (1976) and Olsson (1998) obtained similar results to ours in King Penguin colonies of different sizes (29% mate retention in a 56,000-pair colony and 19% in a colony of 150 individuals, respectively; data on colony size in Voisin [1971] and Olsson [1998]). Another consequence is that divorce would be no more than a by-product, with divorced in-dividuals making the best of a bad situation.

Divorce and mate choice.—We failed to find an advantage of mate retention or a cost of di-vorce. Furthermore, the combination of factors noted above was insufficient to explain the high incidence of divorce when asynchrony was low. Olsson (1998) explained this phenomenon by speculating that many birds previously had mated with a lower-quality partner than they could have obtained had they managed earlier to store enough fat prior to the fasting period; under these conditions, divorce would be adap-tive. Olsson (1998) predicted that, in the ab-sence of time constraints caused by the fat-stor-age problem, birds would choose a partner of as high a quality as possible in an "ideal-free" manner (Fretwell and Lucas 1970). Olsson (1998) suggested that the absence of territorial behavior in King Penguins would enable indi-viduals to assess potential partners rapidly and with low cost when moving through the colo-ny. Thus, they could choose the most suitable mate as long as they could afford to sample mates, because of fat-storing constraints. These predictions supported the "better-option" hy-pothesis (Ens et al. 1993, Choudhury 1995), which states that one member of a pair initiates

divorce if it has the opportunity to improve its reproductive success by obtaining a higher-quality mate.

Our results suggest that mate quality was not linked to return date for high-quality King Penguins, although the latter tended to arrive first and to have the highest breeding success. The fact that these tendencies were not statistically significant may be explained by small sample size. In contrast, high-quality individuals were particularly attractive for low-quality ones, which had more difficulty obtaining them as partners as time elapsed. Yet, late breeding increases the probability of failure, independent of quality (Olsson 1996). Therefore, our results are consistent with the "ideal-free" mate-choice hypothesis. However, the proportion of high-quality individuals and evenly matched partners must not vary greatly between different colonies, as suggested by divorce rates similar to ours in South Georgia and in Barrat's (1976) colony. In the more synchronously breeding Emperor Penguin, the lack of data on individual quality precludes firm conclusions. Yet, the absence of territoriality reaches its highest level in this species (Stonehouse 1953); breeders walk with their egg or chick on their feet and congregate in "huddles" when the weather becomes especially harsh (Prévost 1961, Isenmann 1971). Thus, searching for a new partner should not be very costly for this species either. Moreover, the number of male partners available per unpaired female decreases as time elapses, which enabled Isenmann and Jouventin (1970) to attract up to 20 unpaired females simultaneously by using the playback of a male's calls during the last days of the courtship period. At this time, these females probably would have paired with the first available male. Consequently, Emperor Penguins may also perform mate choice in an "ideal-free" manner. Our conclusions are consistent with Olsson's (1998). In both species of *Aptenodytes* penguins, only some individuals (probably the latest arrivals) would seek a partner, not to improve their breeding success (which has a greater chance to decrease as time elapses), but to limit the risk of not breeding altogether.

Conclusion: Why is divorce so common?—We failed to discover a link among divorce, breeding experience, and breeding failure in the previous year, giving no support to the "incom-

patibility" hypothesis (Coulson 1966, Rowley 1983). Yet, it should be more interesting to test this hypothesis using the true breeding experience (i.e. that since individuals have entered the breeding population) combined with quality. The behavioral plasticity of *Aptenodytes* penguins is in accordance with predictions of the "better-option" hypothesis, as previously suggested for King Penguins by Olsson (1998). Our results concerning the latest-arriving individuals can be explained by the "musical-chairs" hypothesis, which states that individuals settle on the best territory available; a King Penguin returning too late will find its previous breeding area occupied and will have to settle elsewhere in the colony (Barrat 1976). This hypothesis predicts that divorce "may be a side-effect of differential arrival of the sexes" (Choudhury 1995). In the Emperor Penguin, males would replace territories as "chairs," at least in some cases.

In most cases, however, access to potential partners does not seem very difficult nor time consuming for King Penguins and Emperor Penguins, which have to face two conflicting constraints: (1) they have long breeding cycles relative to their large body size (Stearns 1992); and (2) their breeding schedule is severely constrained such that they must save as much time as possible to rear their chick within the limits set by environmental conditions. In light of this scenario, Olsson (1998) may not have devoted sufficient attention to the role of the absence of nesting sites and territorial behavior on mate retention. Hence, we suggest that divorce is common in *Aptenodytes* penguins, not only because it is not costly, but because in the absence of nest sites that serve as meeting points (e.g. Hinde 1956, Morse and Kress 1984), mate retention could be maladaptive. *Aptenodytes* penguins seem to have adopted an "optimal divorce" strategy (McNamara and Forslund 1996) that enables them to adapt their breeding cycles to seasonal changes in their environment.

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