Bird Study (2011) **58,** 160–170

Differential migration in the polygynandrous Alpine Accentor *Prunella collaris*

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Capsule Differential migration by sex and age occurs in the Alpine Accentor *Prunella collaris*.
Aims To characterize the wintering phenology of migrating Alpine Accentors, and to test for differences in sex and age ratios between wintering sites.
Methods Alpine Accentors wintering at low elevation, in Mediterranean France, were monitored (census, ringing) over four winters. Individual arrival date, duration of stay and departure dates were analysed according to sex and age. Within-day use of the site was characterized. Results were combined with previously published data to test for differential migration.
Results Post-breeding migration was recorded in November. Yearlings arrived 22 days later than adults at the wintering site. Females stayed longer (108 days) than males (77 days). The study site – a picnic place – was mainly used by the birds in the afternoon. Males departed earlier (22 February) than females (7 March). The inter-annual return rate was 0.61 (without transients).
Conclusion Combining these results with available estimates of age and sex ratios from other wintering populations revealed that female and yearling Alpine Accentors are more prone to migrate than adult males. Differential migration probably results from the ecological selective pressures faced by the species, particularly their high-altitude breeding grounds and their polygynandrous mating system.

When the non-breeding environment imposes different selective pressures according to sex or age, differential migration within a species is predicted, resulting in the different classes of individuals being segregated in different wintering habitats (Ketterson & Nolan 1983, Kissner *et al.* 2003). Seven hypotheses have been proposed to explain the evolution of differential migration between sexes (including protandrous return to breeding sites [Morbey & Ydenberg 2001]). Four of these hypotheses have received some support from studies involving birds (reviewed in Coppack & Pulido 2009; Saino *et al.* 2010). The 'mate opportunity' hypothesis requires that the early settlement of males at breeding grounds increases their mating opportunities. If first arrival is a reliable indicator of male quality for females, then mate choice would also select for protandry (the 'mate choice' hypothesis). This hypothesis is reinforced when the 'rank advantage' hypothesis operates, i.e. when the date of arrival determines the social rank of males and that females favour highly ranked mates. The 'differential susceptibility' hypothesis (also called 'body size' hypothesis) relies on the greater resilience of males to adverse environmental conditions than females because of their larger size (but the relatively small size dimorphism between sexes in most birds limits the generality of this hypothesis). Finally, independently of any sexual selective pressure, the dominated sex, usually female, may just be selected to emigrate from breeding territories during the non-breeding season (the 'social dominance' hypothesis; related to the 'constraint hypothesis'), while males would monopolize the limited, local food resources.

Despite the importance of all these selective pressures on fitness faced during the non-breeding season (Myers 1981, Ketterson & Nolan 1983, Marra *et al.* 1998), their impact on the evolution of mating systems in birds is commonly neglected. This is particularly the case for polygynandry. Polygynandry is the mating system in which females simultaneously mate with several males, and males provide parental care to the offspring of several females. Alpine Accentors *Prunella collaris* have been a major biological model to study the selective

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pressures that drive the evolution of polygynandry (Davies *et al.* 1995, Hartley *et al.* 1995, Nakamura 1995c, Davies & Hartley 1996, Heer 1996, Nakamura 1998a,b). The consensual scenario gives a central role to the spatio-temporal variation of food availability during the breeding season. Alpine Accentors breed at high altitude (above 1500 m [Cramp 1988]). The alpine ecosystem is constraining because food is heterogeneously available in space and time (Antor 1995, Davies *et al.* 1995). This heterogeneity constrains Alpine Accentors to forage in groups within large home ranges (Davies *et al.* 1995, 1996, Nakamura 1995c, Davies & Hartley 1996, Heer 1996). The environmental constraint is not quantitative food limitation (Nakamura 1995a, 1998b), but patchily distributed spots of food scattered over a wide range (Davies *et al.* 1995, Nakamura 1995c; but see Davies & Hartley 1996) with marked temporal fluctuations mainly driven by local differences in the timing of snow-melting. This induces asynchrony in breeding timing between female territories (Praz 1976, Davies *et al.* 1995, Martín-Vivaldi *et al.* 1995, Nakamura 1995c, Heer 1996; but see Nakamura 1995b, 1998b, Davies *et al.* 1995). Such a spacing system has the result that mating events are hardly controlled by individuals, and the control of mating events becomes the limiting resource. Males compete for female access, and females compete for breeding site and male parental care. This results in high sexual competition and conflicts of interest between the sexes (with very intense sperm competition [Nakamura 1990a, 1998a, Hartley *et al.* 1995, Davies *et al.* 1996, Chiba & Nakamura 2002, 2003]), and between dominance ranks within sexes (Nakamura 1990a, 1998a, Davies *et al.* 1995, 1996, Langmore *et al.* 1996), with dominance rank being mainly determined by age (Davies *et al.* 1995, Heer 1996, Nakamura 1998a; Table 1). The amount of mating access translates into paternity share. Males then adjust their investment in parental care according to the mating opportunities they had per female (Hartley *et al.* 1995, Davies *et al.* 1996, Heer 1996). The probability of gaining access to an alpha rank in the lifetime of a male (only 21% [Nakamura 1998a]) is constrained by the linear dominance hierarchy and limited to death events of higher ranked individuals. Thus, subordinate males compensate for low access to fertile females by maximizing opportunistic copulations (i.e. polygyny [Nakamura 1998a]). Females attempt to compensate for the cost of shared male care on reproductive success by increasing the number of males providing parental care to their chicks (Davies *et al.* 1996, Langmore *et al.* 1996, Nakamura 1998a, 1998b; but see Davies *et al.* 1995). For this, they need to increase mating opportunities with subordinate males (i.e. polyandry [Davies *et al.* 1995, 1996, Hartley *et al.* 1995, Nakamura 1998b]). Avoidance of monopolization by the alpha male is achieved by between-female synchronization of their fertile periods (Davies *et al.* 1995, Nakamura 1998b; but see Heer 1996) and by female secondary sexual characters (Nakamura 1990a, 1995c, Langmore *et al.* 1996, Chiba & Nakamura 2002). Other hypotheses explaining the evolution of polygynandry in Alpine Accentors have not been substantiated (competition for breeding site [Nakamura 1995a, Davies & Hartley 1996]; territory defence advantage [Davies & Hartley 1996]; reduced female harassment [Davies *et al.* 1996, Nakamura 1998b]; genetic benefits [Hartley *et al.* 1995, Davies *et al.* 1996, Nakamura 1998b]).

Polygynandry is thus the result of strong conflicts of interest between sexes and among age classes (Table 1), induced by environmental constraints during the breeding season. Differences between individuals in ecological constraints during the non-breeding season may also come into play, but their relationships with polygynandry and high altitude reproduction have been ignored (but see Nakamura *et al.* 1996). Studies of the non-breeding ecology of Alpine Accentors were mainly conducted at or close to breeding grounds (Appendix 1). Hence they address only sedentary wintering individuals who perform no, or at best local, altitudinal movements (Cramp 1988, Martí *et al.* 1989, Davies *et al.* 1995, Heer & Fraenkl 1999). However, Alpine Accentors are known to extend their range considerably in winter and part of the population migrates regularly (Cramp 1988). The wintering ecology of these migrating Alpine Accentors is poorly known (Martí *et al.* 1988, 1989, Heer 1999), and only the insular Japanese populations have been studied in any detail (Nakamura *et al.* 1996, Nakamura & Nishiumi 2000). No study is available for Eurasian migratory Alpine Accentors.

In an attempt to fill this gap of information on the wintering biology of the Alpine Accentors, I monitored individually colour-marked Alpine Accentors wintering at a low altitude site in the French Mediterranean region. Since the closest known breeding grounds were 170 km away (Lebreton 1994) these birds should be considered migratory. Results from this study, combined with an extensive review of published data, reveal differences in migration and wintering strategies (timing of wintering, site fidelity) between sexes and age classes for the Alpine Accentor. These differences are discussed in the context of the evolution of differential

Table 1. Differences between ages and sexes in life history traits and fitness components in Alpine Accentors *Prunella collaris*.

Trait	Yearling versus adult	Male versus female	Age criteria	Details and references
Migration	≠	≠, =,≠	1Y	Heer (1996), Nakamura & Nishiumi (2000), present study
Departure date from breeding ground	<		1Y	Martí *et al.* (1989)
Arrival date to wintering ground	>	=	1Y	Present study
Departure date from wintering ground	=	<	1Y	Present study
Arrival date to breeding ground	>	<	1Y	Nakamura (1995b), Heer (1996)
Breeding group fidelity		<, =	–	Davies *et al.* (1995), Nakamura (1995c)
Date of maximum cloacal protuberance	>		1Y	10–16 days (Nakamura 1995b)
Laying date	>		1Y	14.6 days (Davies *et al.* 1995), 19 days (Nakamura 1995b)
Clutch size	<		1Y, Rank, Age	Nakamura (1995d, 1998b), Langmore *et al.* (1996)
Female access to dominant male	<		1Y, Age	32% versus 75% (Davies *et al.* 1996, Langmore *et al.* 1996)
Male access to females	<		Rank	Hartley *et al.* (1995)
Copulation interruption	>		Rank	Nakamura (1998b)
Spring food limitation	>	=	1Y	Nakamura (1995a, 1995b)
Nest failure	>		1Y	18% versus 59% (Nakamura 1995b, d)
Nest-building and incubation		<	–	Davies *et al.* (1995), Nakamura (1995c, 1998b)
Nestling mass	<		1Y	Nakamura (1995d)
Number of breeding attempts	<		1Y	1.55 versus 1.95 (Nakamura 1995b, d)
Number of copulation mates	<		Rank	4.0 versus 2.2 (Nakamura 1998b)
Number of males providing food	<		Rank	Nakamura (1998b)
Reproductive success	<		1Y, Age	Nakamura (1995d), Langmore *et al.* (1996)
Body size	<	>	1Y	Cramp (1988), Nakamura (1990b), Davies *et al.* (1995), Heer (1999), present study
Social hierarchy	>	>	Age, Size	Davies *et al.* (1995), Heer (1996), Langmore *et al.* (1996), Nakamura (1995b, 1998a, b), Nakamura *et al.* (1996)

Age criteria are the real age; yearlings (1Y) versus adults; the rank (since rank is mainly determined by age [Davies *et al.* 1995, Heer 1996, Nakamura 1998a]); or the size, since it increases with age. < holds for lower than, < for higher than, = for no difference between, and 'sign different' for different between.

migration in response to high altitude reproduction and polygynandry.

MATERIALS AND METHODS

Study site and survey design

During winters 1999–2000 to 2002–03, from 1 November to 1 April, I monitored on a bi-weekly to monthly basis (n = 36 visits) a group of Alpine Accentors wintering at Pic Saint-Loup, southern France (43°47′N, 3°49′E). The habitat is an abrupt 250 m-high, 3 km-long cliff on the northern slope, rocky ridge along the summit and a continuous Oak *Quercus ilex* forest on the southern slope. This mountain is 658 m asl, and 29 km from the sea. The climate is Mediterranean, with an average of less than one week of snow cover per winter. The survey area was restricted to the summit of the mountain, i.e. a 30 m-long and 5 m-wide area, where Alpine Accentors regularly forage on the food leftovers of hikers. Visits lasted on average 3 hours 29 minutes ± 1 hour 45 minutes sd; i.e. twice the time estimated to be needed to record all birds present during a visit (1 hour 35 minutes ± 1 hour 14 minutes sd). In 79% of the visits, all birds present around the top of the mountain during a given visit were either captured or resighted (as in Nakamura & Nishiumi [2000]). For the remaining 21% of visits, at least ten individuals were missed. Seven of them were likely captured on the subsequent visit, and three individuals have never been captured (two in November, one in March).

Birds were captured with a bread-baited falling-trap. Each bird was individually marked with colour rings and measured (Table 2). Sex was determined with the discriminant function provided by Heer (1999). Birds in their first year (yearlings) were distinguished from ≥ one-year old individuals (hereafter, adults) by juvenile unmoulted greater covert feathers and wear of the primary feathers (Svensson 1992, Heer 1999). Faded tongue-spots proved to be an unreliable age criterion. They were present in three out of 17 yearlings.

Table 2. Morphometric measurements (mean ± sd) of Alpine Accentors *Prunella collaris* captured at Pic Saint Loup, southern France, according to sex and age.

	Male		Female	
Trait (method; precision)	Yearling (n = 4)	Adult (n = 4)	Yearling (n = 11)	Adult (n = 5)
Wing (max. chord; ± 0.5 mm)	105.5 ± 1.6	108.8 ± 1.4	97.9 ± 1.3	100.1 ± 1.8
Tail (± 0.5 mm)	67.3 ± 0.6	70.3 ± 1.8	60.7 ± 1.3	63.4 ± 2.4
Tarsus (± 0.1 mm)	25.6 ± 0.8	25.3 ± 0.5	25.0 ± 0.6	24.7 ± 0.5
Bill (to feathering; ± 0.1 mm)	13.0 ± 0.6	13.2 ± 0.7	13.6 ± 0.5	13.6 ± 0.6
Bill (to nostril; ± 0.1 mm)	9.6 ± 0.3	9.5 ± 0.3	9.5 ± 0.3	9.7 ± 0.3
Bill depth (± 0.1 mm)	3.9 ± 0.2	4.1 ± 0.2	4.0 ± 0.2	4.0 ± 0.1
Body weight (± 0.5 g)	38.8 ± 2.1	38.5 ± 2.3	34.5 ± 1.4	35.2 ± 1.9
Fat score (1–4 units)	1.8 ± 1.0	2.5 ± 0.6	2.2 ± 0.8	2.6 ± 0.5

Population structure, phenology, and inter-annual return rate

Sex and age ratios were expressed respectively as the ratios of males to females, and yearlings to adults. Individual arrival and departure dates were defined by the dates of first presence and first absence per winter. For the seven individuals that could not be captured on the day of their first observation, the arrival date used in the analysis was the date of first sighting instead of the date of first capture. The duration of stay was the difference in days between these two dates. The fixed effects of sex, age, and their interaction on duration of stay, arrival and departure dates were tested. Eight individuals (33%) were recorded during several winters. This non-independency among data points was accounted for in the analyses of phenology data by the use of linear mixed models (NLME package for R [Zuur *et al.* 2009]), including a random term for between-individual variations.

The return rate was defined as the probability to be resighted in the following winter at the study site. Dependency on sex, age, and their interaction were tested by likelihood-ratio tests with logistic regression models.

Individuals were a mixture of migrants (transient), which rapidly left the site after their first capture and winterers which stayed throughout the winter. To avoid the bias induced by transiency on wintering phenology parameters only individuals that stayed more than 30 days (see Results) were considered when computing the duration of stay and the departure date.

Within-day use of the study site

To test for within-day variation in use of the study site, I computed (1) the time elapsed between my arrival at the survey area and the time when I observed the first accentor; and (2) the number of contacts per individual per hour. A contact is defined as the arrival of a bird at the survey area, irrespective of whether it had already been observed in the same hour or not. The effects of the hour of day, sex and age were estimated respectively with (1) a log-normal regression, adjusted for overdispersion; and (2) a GLMM for Poisson data, adjusted for overdispersion, and where individual identity and days were entered as random effects (LME4 package for R [Zuur *et al.* 2009]). The most parsimonious temporal pattern for the effect of the hour of the day (linear, quadratic, cubic, exponential, log), was identified by AIC-based model comparisons. All statistical tests were built with R 2.8.1 (© 2008, The R Foundation for Statistical Computing).

RESULTS

Twenty-four alpine accentors were marked (17 yearlings, seven adults; between three and 10 individuals were missed), generating 247 resightings. Morphometric measurements are summarized in Table 2. Two individuals remained unsexed according to the discriminant function of Heer (1999). The average wintering group size was about five individuals (Fig. 1). The average sex and age ratios were 0.55 males per female, and 0.95 yearlings per adult per winter (Table 3).

Arrival dates spanned from November to January, with a mean arrival on 30 November ± 26 days sd. Yearlings arrived on average 22 days later than adults (14 December ± 32 sd versus 23 November ± 17 sd; $F_{1,21}$ = 4.479, P = 0.046). Both sexes arrived at the same time (males, 7 December ± 32; females, 27 November ± 21; $F_{1,18}$ = 1.812, P = 0.195), although yearling males would arrive later than others (28 December versus 22–29 November; sex–age interaction, $F_{1,17}$ = 4.698, P = 0.045).

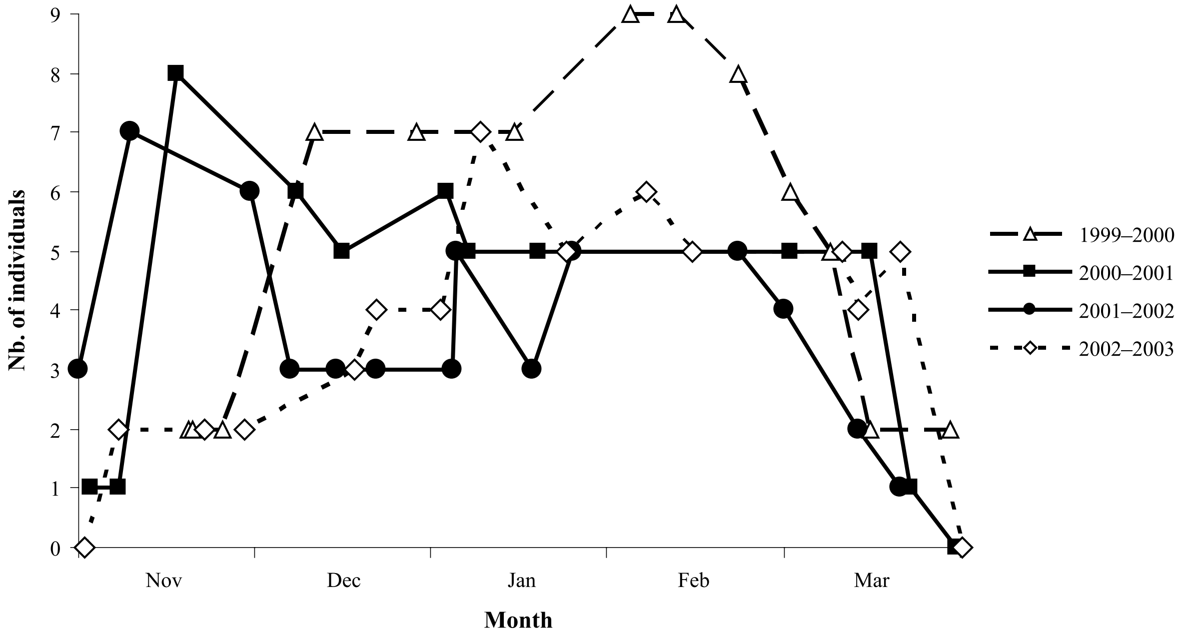

Figure 1. Minimal number of Alpine Accentors *Prunella collaris* observed per visit to the study site at Pic Saint Loup, southern France (including both marked and unmarked individuals).

Table 3. Numbers of Alpine Accentors *Prunella collaris* by sex, age and winter (marked individuals only) studied at Pic Saint Loup, southern France.

Winter	1999–2000	2000–01	2001–02	2002–03	Total
Male	4	3	2	3	12
Female	5	6	5	6	22
Yearling	6	3	4	4	17
Adult	4	6	4	5	19

The peaks in group size observed in November (2000–01, 2001–02; Fig. 1) were probably because of the occurrence of migrating birds which were migrating beyond this site (transients) during this month. Indeed, birds seemed unstable at this period, performing regular high and/or distant flights, with contact calls that were not recorded in later months. To discriminate transients from winterers, I relied on the bimodality of the distribution of the proportion of the winter spent at the study site per individual (Fig. 2): individuals staying more than 20% (corresponding to 30 days) of their winter at the study site were considered as winterers (n = 21 individuals), and others as transients (n = 10; this number includes an unknown number of individuals that were not transients but winterers that died). The percentage of transients was 38% in November (n = 18), and 17% (n = 23) in December (Fisher's exact test, P = 0.146).

The duration of stay spanned from 0 to 143 days, with five individuals disappearing before the subsequent visit. The average duration of stay of winterers was 96 days ± 33 sd. Females stayed longer than males (respectively, 108 ± 31 sd and 77 ± 27 sd; $F_{1,10}$ = 5.647, P = 0.039, Ps > 0.338 for other effects). In most cases, presence at the study site was continuous, i.e. birds were recorded on all visits between their arrival and departure dates. In only 13 out of 144 cases (i.e. visits per wintering bird), an individual temporarily moved to another wintering site, and then returned to the study site before the end of the winter. In seven out of these 13 cases (three birds), the alternative wintering site was at 2.05 km, at the closest village from the Pic Saint Loup (Cazevieille, 298 m asl).

Departure dates were more synchronized than arrival dates and essentially occurred during the second half of March (Fig. 1). The mean departure date of wintering individuals was 7 March ± 22 sd. Males departed earlier than females (22 February ± 19 sd versus 17 March ± 15 sd; $F_{1,10}$ = 5.867, P = 0.036, Ps > 0.192 for other effects).

The inter-annual return rate was 0.44 (n = 31 individuals). No dependency on age and sex could be detected (all Ps > 0.333). The return rate of winterers was 0.61 (n = 18) and the return rate for transients was 0.11 (n = 10). All returning individuals did so in subsequent winters, with no evidence for temporary change of wintering site.

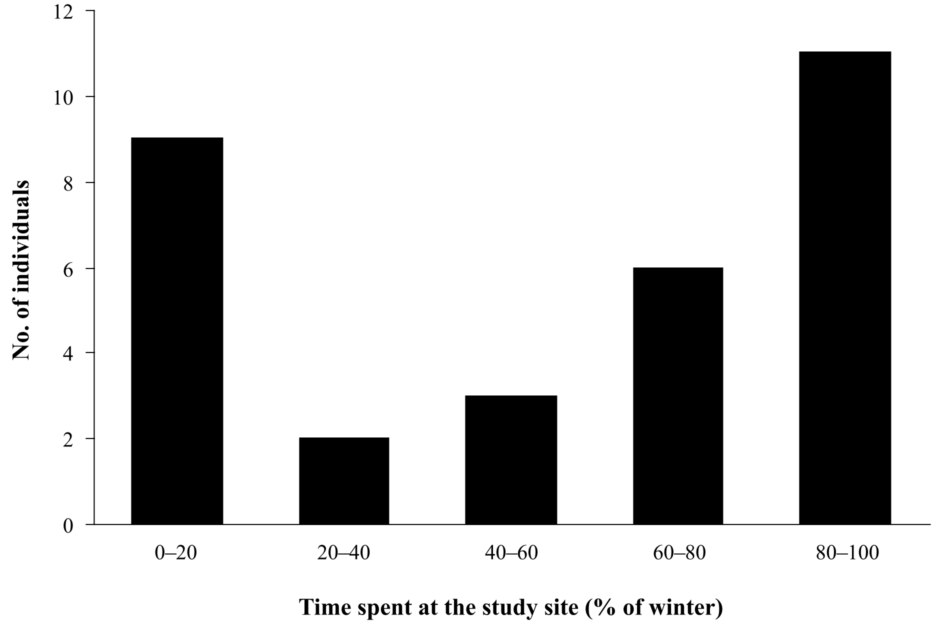

Figure 2. Distribution of the proportion of winter duration that individuals spent at the study site at Pic Saint Loup, southern France. This proportion is computed as the duration of stay per winter per individual, divided by the number of days between the arrival date and 1 April.

Frequency of the birds' visits to the study site increased throughout the day. The time elapsed between my arrival at the survey area and the first bird record decreased with the hour of the day (linear effect on the log-scale, $F_{1,29} = 15.905$, $P < 0.01$; Fig. 3a). The log-transformed number of contacts per individual per hour also significantly increased with the hour of the day (linear effect, $F_{1,273} = 23.583$, $P < 0.001$; Fig. 3b), with no difference between sex and age classes (all *P*s > 0.225). This frequency of visit rate varied among individuals (random effect, $\chi^2(1) = 47.948$, $P < 0.001$), indicating that some individuals visited the study area more than others.

DISCUSSION

Alpine Accentors vary in their wintering strategies. Some individuals are resident, performing only local altitudinal movements (Praz 1976, Martí *et al.* 1989, Martín-Vivaldi *et al.* 1995, Heer 1996, Heer & Fraenkl 1999). Some individuals migrate to lowlands (up to 250 km, Nakamura *et al.* 1996, at least 170 km in the present study). These differences have been poorly documented, and the wintering phenology of migrants has never been characterized. Post-breeding migration lasts from mid-October (Japan [Nakamura 1998b]) to mid-November (Europe [Christen 1984, Cramp 1988, present study]). Migrants reach their wintering ground by late October to mid-November (Christen 1984, Schmidt 1985, Cramp 1988, present study). Once settled at the wintering site Alpine Accentors are sedentary (Nakamura *et al.* 1996, present study) with some individuals exploiting feeding sites a few kilometres apart (Martí *et al.* 1988, Gstader & Tschaikner 1991, Heer & Fraenkl 1999, present study). At our study site, Alpine Accentors frequented the area mainly in the afternoon, a pattern already observed in other mountain species foraging on the leftovers of hikers (Delestrade 1995). In the morning, they seemed to forage in the cliff areas on the northern side of the mountain. Departure from wintering grounds starts in February (Schmidt 1985, present study). Pre-breeding migration peaks in early April (latest records in May [Christen 1984, Schmidt 1985, Cramp 1988]). The high inter-annual return rate (0.61, $n = 9$ [present study]; 0.83, $n = 12$ [Nakamura *et al.* 1996]) suggests that migratory birds are largely faithful to their wintering ground: assuming an annual survival rate of 0.6–0.8, 75–100% of surviving individuals would return to the same wintering place. Alpine Accentors are also known to be highly faithful to their breeding sites (annual return rate: 0.52, $n = 59$ [Davies *et al.* 1995]; 0.70, $n = 123$ [Nakamura 1998b; Nakamura 1995a,c, Heer 1996]).

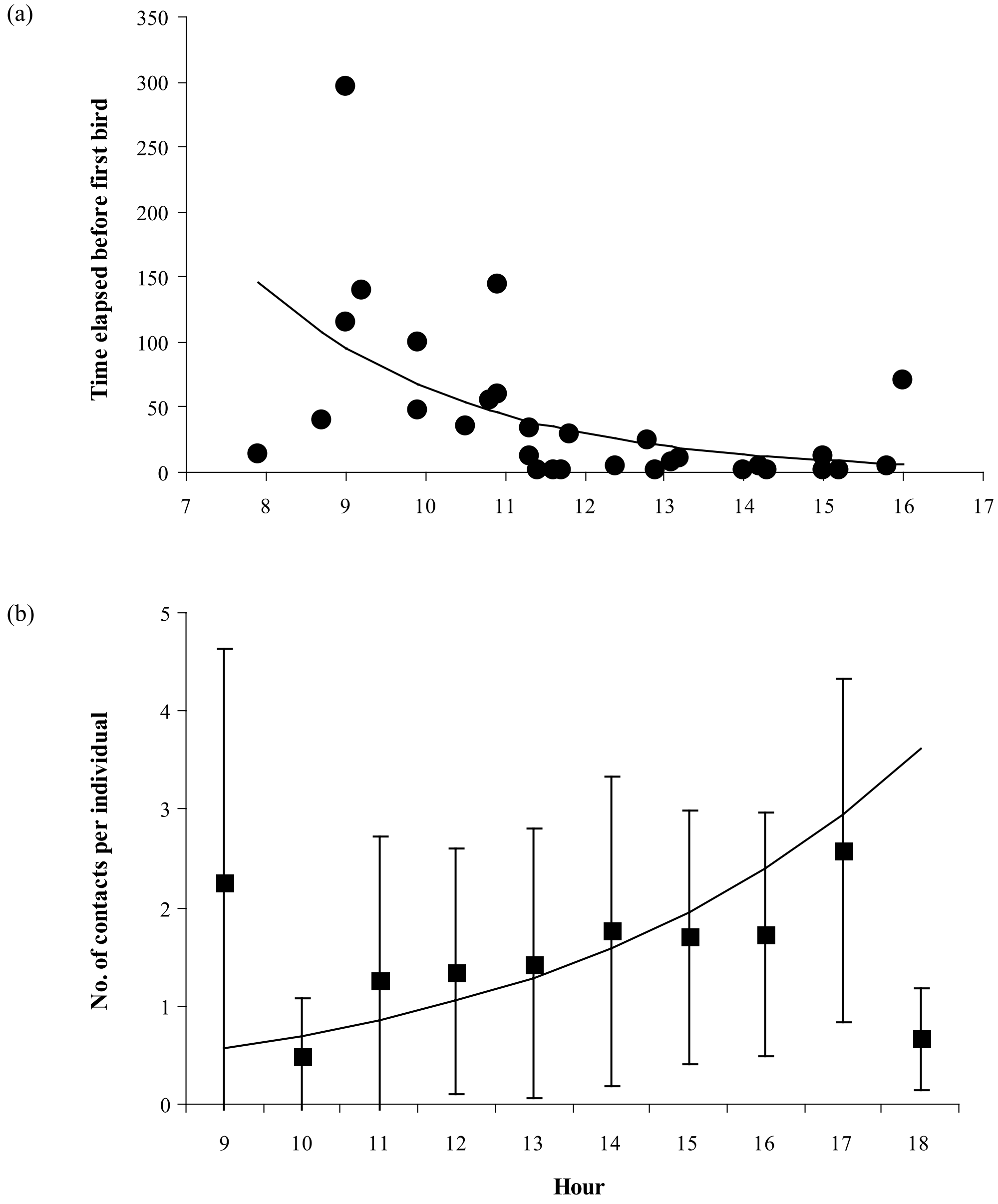

Figure 3. Frequency of visits to the study site at Pic Saint Loup, southern France by Alpine Accentors *Prunella collaris* as a function of the hour of the day measured by (a) the time elapsed (in minutes) between the start of observations at the study site and the first recorded bird; and (b) the mean (± sd) number of contacts per individual per hour. The lines represent the predicted values with the GLMs including a linear effect of the hour.

Differential migration by sex is shown by different components of the population according to their wintering biology. Resident birds are mainly males (73 males per female, n = 74; [Aichhorn 1969, in Martí *et al.* 1989]; five males per female, n = 25 [Martí *et al.* 1989]; 1.89 males per female, n = 55 [Martín-Vivaldi *et al.* 1995, Heer 1996, Heer & Fraenkl 1999]), whereas migratory birds include a large proportion of females (0.55 males per female, n = 34 [present study]; 0.91 males per female, n = 111 [Nakamura & Nishiumi 2000]; 1.67 males per female, n = 16 individuals [Nakamura *et al.* 1996]). These between-site differences in sex ratio are significantly explained by the migratory status of birds (ANODEV with models 'site' versus 'migratory status', $F_{1,10}$ = 6.632, P = 0.028; see Appendix 1). This results in an altitudinal gradient in sex ratio during

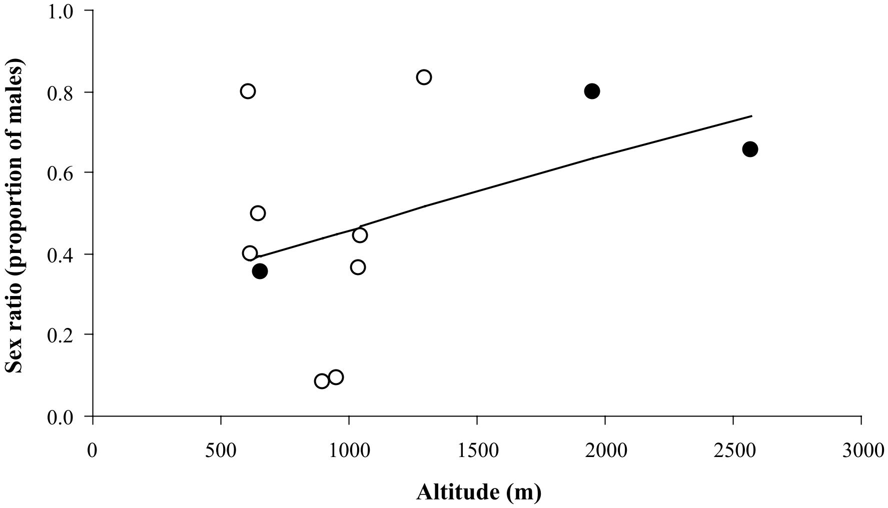

Figure 4. Sex ratio of wintering groups of Alpine Accentors *Prunella collaris* according to altitude, for Europe (•; n = 3 sites) and Japan (○; n = 9). The line represents the predicted proportion of males with the logistic regression including a linear effect of altitude.

winter (ANODEV with models 'site' versus 'altitude', $F_{1,10}$ = 26.444, P = 0.0004; Fig. 4). This altitudinal gradient was not found within Japan (Nakamura & Nishiumi 2000). This may be explained by the fact that groups wintering close to their breeding grounds were not included in this study, and/or because the population of Alpine Accentors in Japan may be more prone to migrate than European ones (winter sex ratio, 0.91, n = 111, $\chi^2(1)$ = 0.225, P = 0.635). The non-breeding phenology also differs between the sexes, with males departing earlier from the wintering ground (present study) and arriving earlier at the breeding ground (Table 1).

Differential migration by age is also evidenced. Resident individuals are mainly adults (0.45 yearlings per adult, n = 74 [Aichhorn 1969, in Martí *et al.* 1989]; 0 yearlings per adult, n = 25 [Martí *et al.* 1989]), whereas an equal proportion of yearling and adults migrate (0.95 yearlings per adult, n = 36 [present study]; one-sided Fisher's exact tests, respectively P = 0.076 and < 0.001). Adults stay closer to the breeding grounds than yearlings. Yearlings depart earlier from breeding grounds than adults (Table 1) but arrive later at their wintering ground (present study). In spring, yearlings depart from the wintering ground at the same time as adult (present study) but they arrive later at the breeding grounds and start breeding later (Table 1).

Differential migration by sex and age can be related to the selective pressures that drive the maintenance of polygynandry in Alpine Accentors (cf. Introduction; Table 1). It can be argued that males would increase their reproductive success by arriving early at the breeding grounds. In males the dominance rank seems to be the major determinant of mating strategy and lifetime reproductive success. However, the opportunities to attain a high dominance rank are limited by the death of dominant individuals. Thus, early arrival at breeding grounds may increase the probability to access a higher rank. In males, age differences in non-breeding movements could thus be a direct consequence of the reproductive skew imposed by dominance-mediated access to mates. Overall, if being early on the breeding grounds is necessary to increase dominance rank (the 'rank advantage' hypothesis [Morbey & Ydenberg 2001]), it would explain why individuals with the highest competitiveness and highest benefits of winning sexual competition, i.e. males and older individuals, tend to be resident and/or to depart earlier from wintering grounds. Additionally, early arriving males are advantaged because they are more likely to mate with early arriving females, which generally have the highest reproductive effort and success (Table 1; the 'mating opportunity hypothesis' [Morbey & Ydenberg 2001]). In the opposite direction to males, females would increase their reproductive success by arriving later than males at the breeding grounds. This delay would maximize among-male competition and improve their chances to secure paternities and parental care from both dominant and subordinate males (the 'mate choice hypothesis' [Morbey & Ydenberg 2001]).

Dominance hierarchy is a major social feature in Alpine Accentors: males dominate females (year-round) and older individuals dominate younger ones (Table 1). Dominance avoidance is probably one of the mechanisms that drive differential migration (reviewed in Kokko 1999, Marra 2000, Morbey & Ydenberg 2001). Social rank- and size-regulated access to food may induce food limitation in dominated individuals, i.e. essentially females and yearlings, particularly during the winter food shortage (Table 1). This despotic access to food may enhance the handicap of small body-size in females and the lower energetic efficiency in yearlings (Kissner *et al.* 2003; higher susceptibility to food limitation; Table 1), thus selecting for differential migration according to competitiveness for food access (the 'social dominance' or 'constraint' hypothesis [Coppack & Pulido 2009]). Indeed, little antagonistic interactions were recorded among individuals that winter far from breeding grounds (Nakamura *et al.* 1996; only three agonistic encounters out of 191, present study).

In early spring (May–June) reproduction is constrained by the timing of snow melting on the breeding grounds (Praz 1976, Davies *et al.* 1995, Martín-Vivaldi *et al.* 1995, Nakamura 1995c, Heer 1996). This transition period is marked by strong food limitation and high energetic demands, as evidenced by the high proportion of the time allocated to foraging (68% [Nakamura 1995c]), the higher frequency of visits to artificial feeding places (Nakamura 1995a,d) and higher frequency of group foraging than later in the season (Figure 7 in Nakamura 1995c), and the higher frequency of visits to mountain refuges in spring than during the rest of the year (Martín-Vivaldi *et al.* 1995). This food limitation has more of an effect on yearling than older individuals (Nakamura 1995a,b; Table 1), although it would not affect their territory size, reproductive success and mating system (Davies *et al.* 1995, Nakamura 1995a, 1998b). Hence, young individuals would have no advantage in arriving early on breeding grounds because of climate instability and food limitation (Table 1). Since yearling males are unlikely to obtain a high social rank (and the corresponding reproductive benefit) on their first breeding attempt, and yearling females have poor access to dominant males (Table 1), it would explain why yearlings return later to breeding grounds than adults (Table 1).

To conclude, the life cycle of Alpine Accentors is driven year-round by marked differences in ecological and social constraints among sexes and age classes (Table 1). During the breeding season conflicts of interest in maximizing individual fitness oppose males to females, and also impose a strong reproductive skew according to age (driven by dominance relationships). In this study it has been shown that differential migration by sex and age occurs during the non-breeding season. Dominance-mediated access to food, interacting with the harsh winter climate at high altitudes, probably selects for migration in subordinate and less energetically efficient classes of individuals. Alpine Accentors appear to be an exception among polygynandrous species; other polygynandrous species appear to maintain their social bonds year-round.

ACKNOWLEDGEMENTS

I am very grateful to A. Delestrade, F. Archaux and G. Balança for help with fieldwork, and inspiring discussions, and to the two anonymous reviewers who provided insightful comments on the manuscript. I thank the 28 persons who sent resightings of marked birds. Ringing license was delivered by CRBPO (Muséum National d'Histoire Naturelle, France).

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(MS received 16 July 2010; revised MS accepted 26 November 2010)

APPENDIX 1 DETAILS OF STUDIES OF ALPINE ACCENTORS *PRUNELLA COLLARIS*

Country	Locality	Geographical coordinates	Altitude (m asl)	Season	Distance (km)	References
Austria	Patscherkofel	47°13′N, 11°28′E	2264	NB	0	Gstader & Tschaikner (1991)
Austria	Salzburg area	47°48′N, 13°05′E	–	NB	0–10	Martí *et al.* (1989)
France	Mont Valier	42°49′N, 01°04′E	1960–2260	B	0	Davies *et al.* (1995, 1996), Hartley *et al.* (1995), Langmore *et al.* (1996)
Japan	Yoshino	34°18′N, 135°58′E	560–610	NB	250	Nakamura *et al.* (1996)
Japan	Misaka-Pass	35°33′N, 138°47′E	1250–1350	NB	130	Nakamura *et al.* (1996)
Japan	Koshibu B	35°36′N, 137°59′E	650	NB	–	Nakamura & Nishiumi (2000)
Japan	Koshibu A	35°37′N, 137°59′E	620	NB	–	Nakamura & Nishiumi (2000)
Japan	Tokusa	35°42′N, 138°06′E	1040	NB	–	Nakamura & Nishiumi (2000)
Japan	Ookubo	35°46′N, 137°58′E	610	NB	–	Nakamura & Nishiumi (2000)
Japan	Ichinose B	35°48′N, 138°51′E	950	NB	–	Nakamura & Nishiumi (2000)
Japan	Ichinose A	35°49′N, 138°51′E	1050	NB	–	Nakamura & Nishiumi (2000)
Japan	Mont Norikura	36°06′N, 137°33′E	2600–3026	B	0	Nakamura (1995b, c)
Japan	Mont Norikura	36°06′N, 137°33′E	2600–3026	NB	0	Nakamura (1998b)
Japan	Mont Hakusan	36°09′N, 137°33′E	2000–2702	B	0	Nakamura & Ueuma (1997)
Japan	Ashio	36°39′N, 139°24′E	850–950	NB	185	Nakamura *et al.* (1996), Nakamura & Nishiumi (2000)
Spain	Sierra Nevada	37°04′N, 03°21′W	1750–3398	B, NB	0	Martín-Vivaldi *et al.* (1995)
Spain	Sierra de Gredos	40°15′N, 05°16′W	1870–2550	B	0	Gomez-Manzaneque (1989)
Spain	Sierra de Gredos	40°15′N, 05°16′W	1750–2160	B, NB	0	Martí *et al.* (1988, 1989)
Switzerland	Valais Region	46°10′N, 07°27′E	2300–2800	B, NB	0	Praz (1976)
Switzerland	Valais Region	46°12′N, 07°38′E	2500–2860	B, NB	0	Heer & Fraenkl (1999)
Switzerland	Swiss Jura	47°18′N, 07°31′E	380–1650	NB	10–60	Christen (1984)

B, breeding season; NB, non-breeding season; migratory status has been inferred from the distance to the nearest breeding site (resident when distance <100 km; migratory when distance >100 km).