

ALTERNATIVE MATING TACTICS AND THEIR IMPACT ON SURVIVAL IN ADULT MALE ALPINE IBEX (*CAPRA IBEX IBEX*)

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Adult male Alpine ibex (*Capra ibex ibex*) have been shown to exhibit unusually high survival to relatively advanced ages (>10 years), leading to speculation that males may engage in an energetically conservative reproductive strategy that increases survival. We investigated the extent to which the adoption of alternative mating tactics contributes to the extraordinary survival of adult males in this species. Because basic information on the mating system of Alpine ibex is scarce, we first characterized the temporal and spatial distribution of receptive females. Our observations during 3 consecutive rutting seasons revealed 2 alternative mating tactics. Apparently dominant males monopolized individual receptive females by following and defending them, a tactic known as tending. In contrast, apparently subordinate males tried to achieve temporary access to tended females when the latter started to run, a tactic referred to as coursing. In total, 24 copulations were observed, of which 20 (83.3%) were the result of tending and 4 were the result of coursing. The adoption of the 2 tactics was strongly age-dependent; older males (9–12 years) engaged primarily in tending, whereas younger males (2–6 years) engaged mainly in coursing. Males adopting the coursing tactic spent more time in low-cost and less time in high-cost behaviors than males adopting the tending tactic. Time-budget comparisons with another ungulate species suggested that although tending is a relatively costly tactic, coursing is a low-cost tactic that may contribute to the exceptional adult survival in male Alpine ibex.

Key words: Alpine ibex, *Capra ibex*, life history, mating tactic, reproductive effort, reproductive success, sexual selection, survival

Sexual selection is expected to favor the evolution of alternative male mating tactics when the variance in male fitness is high (Emlen and Oring 1977; Shuster and Wade 2003). This is usually the case when receptive females are aggregated in space but show asynchronous sexual receptivity. Under these conditions, a subset of males may be able to monopolize multiple receptive females, thereby excluding other males from mating. In polygynous ungulates, common male tactics to monopolize 1 or more receptive females are the direct defense of potential mates (Clutton-Brock et al. 1982; Hogg 1987) or the defense of territories on which females reside (Carranza et al. 1990; Clutton-Brock et al. 1988; Von Hardenberg et al. 2000). The successful defense of females or territories is usually restricted to a small number of fully grown and therefore older males (Isvaran 2005; Wolff 2008). Other,

often younger males must resort to alternative reproductive tactics, including abducting estrous females or sneaking copulations when the opportunity arises (e.g., “kleptogamy” in red deer [*Cervus elaphus*—Pemberton et al. 1992] and “coursing” in male bighorn sheep [*Ovis canadensis*—Hogg 1987]) in order to achieve reproductive success.

The observation that alternative mating tactics are often age-dependent (Isvaran 2005; Wolff 2008) may have far-reaching consequences for the life history of a species. Members of long-lived, iteroparous species must decide during each breeding season how much energy to invest in current reproduction versus future survival in order to maximize their lifetime reproductive success (Clutton-Brock 1984; Krebs and Davies 1995). Because reproductive costs and benefits may vary greatly among alternative tactics (Clutton-Brock et al. 1982; Moore et al. 1995; Pelletier 2005; Saunders et al. 2005), the age-dependent adoption of different mating tactics is likely to be a crucial determinant of reproductive success and age-specific survival (see also Loison et al. 1999a).

The Alpine ibex (*Capra ibex ibex*) is a highly sexually dimorphic mountain ungulate. The mating system of this

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species is poorly known (Aeschbacher 1978). A recent study by Toïgo et al. (2007) revealed that, under good environmental conditions, adult male Alpine ibex survived to the advanced age of 10–13 years, with a yearly survival rate of 96–98%. Under poor conditions, survival remained high among males aged 2–8 years but dropped to 85% among males aged 8–13 years. Overall, survival of adult males exceeded the survival of other large herbivores by 5–20%. For example, yearly survival of male bighorn sheep aged 2–8 years was <85% (Bonenfant et al. 2009). Because age-specific mortality patterns among polygynous males are thought to be closely linked to reproductive effort during the mating season (Festa-Bianchet et al. 2000; Stevenson and Bancroft 1995; but see McElligott and Hayden 2000), these findings suggest that male Alpine ibex pursue a comparatively conservative life-history strategy, leading to questions as to whether the age-dependent adoption of alternative mating tactics by male Alpine ibex contributes to their exceptional survival.

To explore this idea, we characterized the mating system of Alpine ibex, with particular attention given to age-related differences in the tactics that males use to compete for females. We present data on the spatial distribution and reproductive cycle of female ibex, both of which contribute to the ecological conditions under which discontinuous mating behaviors are likely to evolve (Shuster and Wade 2003). Based upon work by Aeschbacher (1978) as well as comparative data from other ungulates, we predicted that male Alpine ibex should engage in at least 2 different mating tactics—one in which mostly older males try to monopolize receptive females (tending) and another in which mostly younger males try to achieve temporary access to tended females (coursing). Taking the survival analyses by Toïgo et al. (2007) into account, we expected the latter to be a relatively low-cost tactic that should involve fewer high-cost and more low-cost activities than defending females. In addition to providing the 1st detailed description of the mating system of Alpine ibex, our analyses yield intriguing insights into relationships among mating tactics, energetics, and survival in polygynous ungulates.

MATERIALS AND METHODS

Study population.—The study was carried out in the lightly hunted Cape au Moine population of Alpine ibex north of the village of Les Diablerets in the Swiss Alps (46°22'N, 07°09'E; 1,700–2,550 m elevation). The study area, which measured approximately 13.2 km², consisted mainly of a steep west to east mountain ridge that was characterized by extensive open alpine pastures at higher altitudes (>1,800 m) and by patches of dense spruce forests (*Picea abies*) at lower altitudes (<1,800 m). The area was interspersed with rocky cliffs of varying size. Throughout the winter, the north side of the ridge remained covered by snow, whereas substantial portions of the south side were often free of snow due to solar radiation and avalanches.

Females with young lived year-round in groups of up to 50 animals that were permanently resident in the study area. In contrast, males formed loose groups of variable composition (see

also Villaret and Bon 1998) and at least some males roamed between the study population and 2 adjacent populations. This roaming behavior is also known from other ibex populations (Abderhalden 2005) and seems to be particularly apparent during the prerut period in November–December (see also Parrini et al. 2003). In late autumn and winter (i.e., during the rut), the animals primarily inhabited the steep, south-facing mountain slopes and cliffs that were relatively free of snow, as has been reported for other populations of Alpine ibex (Grignolio et al. 2003).

Sexual dimorphism and life history of Alpine ibex.—Alpine ibex are sexually dimorphic, with adult males being more than twice as heavy as females (95 kg versus 45 kg—Loison et al. 1999b) and possessing much larger horns than adult females (>90 cm versus >30 cm—Lüps et al. 2007). Compared to other ungulates, male Alpine ibex display rather slow yearly growth. As a consequence, body weight does not become asymptotic until the age of 8–9 years, peaking at 11 years of age (Lüps et al. 2007). In contrast, in bighorn sheep and red deer, body weight becomes asymptotic at the age of 6 years (Mysterud et al. 2001; Pelletier and Festa-Bianchet 2006); in Alpine chamois (*Rupicapra rupicapra*), another polygynous mountain ungulate, this occurs by the age of 4 years (Bassano et al. 2003). Male Alpine ibex exhibit an exceptionally good survival of adults up to 8 years of age, and, under good conditions, up to 13 years of age, thereby exceeding survival rates of adults for other large herbivores by 5–20% (Toïgo et al. 2007).

Observation periods and conditions.—Alpine ibex were observed between December and January of 2005–2006, 2006–2007, and 2007–2008. This corresponds to the annual period of rut, when females in the study population were sexually receptive. Each year, rut was determined to have begun on the day when the 1st female was seen to engage in a prolonged association with multiple males. Observations continued for 4–8 weeks after the rut began. During data collection, 1–3 observers monitored the animals visually from dusk to dawn using spotting scopes. The distance between observers and the study subjects varied but was typically between 150 and 1,500 m. In 2005–2006, observations were restricted to a part of the study area that was easily accessible and provided safe observation conditions even when the risk of avalanches was high. In the 2 following years, as snow conditions permitted, observations (with exception of the focal animal observations) were extended to the entire study site.

Identification of individuals and age determination.—In total 121 males (>2 years old) and 30 females (>2–3 years old) in the study population could be individually recognized based on unique characteristics of their horns and coat coloration. In addition, 30 of these animals were individually marked on both ears with colored and numbered ear tags. In the field, observers checked the identity of animals using a booklet containing pictures of all known individuals. In situations in which it was not possible to identify an animal, it was recorded as an unknown male or female. Whenever possible, observers took digital photographs of the animals and later checked their identities by comparing them with photographs of already described animals.

The age of male Alpine ibex was determined by counting the conspicuous annuli on the outer side of the horns (Ratti and Habermehl 1977). In animals that were captured, found dead, or were killed by hunters, this could be done at close distance. For free-ranging unmarked and unknown males, age estimation was carried out directly during observations in the field; for free-ranging unmarked but known (photo-identified) individuals, estimations were performed retrospectively by inspecting all available photographs of these animals. Although the reliability of age estimation for unknown animals could not be quantified, this was possible for some of the known males. Accordingly, the ages of 33 males were 1st estimated from photographs and later confirmed through direct inspection; in all cases, both aging methods yielded the same results, suggesting that age determination for free-ranging male Alpine ibex via photographs is reliable. All aspects of animal capture and data collection were approved by the Swiss Federal Office of the Environment and the Swiss Federal Veterinary Office and conformed to guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Sampling methods.—During all 3 years of the study, daily animal censuses were carried out to collect information on the size and sex–age structure of the population. Because the whole study area was too big to be monitored within 1 day, population-wide censuses were composed of 2 censuses performed on consecutive days.

To obtain data on activity budgets of males, each day observers selected 1–3 known males as focal animals, which were then observed continuously for as long as possible (Altmann 1974). The behaviors recorded included feeding (snout in contact with vegetation), standing, moving (walking and running), and lying down. In addition, multiple courtship behaviors displayed by males were registered, including low-stretch (neck straightened and head held in-plane with the back with the muzzle pointed toward a female), tongue-flick (flicking with tongue toward a female), sniff (sniffing a female, or the site where a female had urinated), lick (licking a female), flehmen (lifting upper lip after having sniffed a female or the site where a female had urinated), touch (touching a female with the snout), self-stimulation (touching penis with snout while standing next to a female), scent-urination (urinating on front legs while standing next to a female), mount attempt (raising front half of body to mount a female), mount (placing the sternum on the female's back), and copulation (subset of mounts in which the abdomen of the male is firmly pressed against the vulva of the female, resulting in a supposed intromission of the penis). Finally, several agonistic behaviors among males were recorded, including evasion (walking away from an approaching male), flight (running away in response to an approaching male), displacement (driving another male away by slowly approaching it), chase (pursuing another male at high speed), rush (running toward another male, usually with slightly lowered horns), horn contact (locking horns with those of another male), horn clash (hitting the horns against those of another male), and homosexual mount (mounting another male). The

activities feeding, standing, and lying down were summarized based on their supposed positive effects on the energetics of animals in the category of “low-cost” behaviors, whereas moving and the various courtship and agonistic behaviors, which can be regarded as energy-intensive investments into reproduction, were pooled in the category of “high-cost” behaviors.

In 2005–2006, focal observations also were conducted on females tended by males to determine which males were associated with the female; the number of mount attempts, mounts, and copulations each female received; and the number of times a female ran away from males.

To obtain information on how males gained and maintained access to receptive females, in each year, all instances were recorded in which a female was attended by ≥ 2 males (of which 1 was the tending male) for at least 10 min. These females were scanned between 1 and 19 times a day ($\bar{X} = 4.1$ scans per day ± 3.5 SD, $n = 211$ females) to record the identifications, ages, and mating tactics of all associated males, as well as to estimate the distances (in female body lengths) between the female and associated males. The 10-min observation period appeared to be sufficient to distinguish between nonreceptive females that were only briefly approached by males (presumably to check their estrous status) and receptive females that were focus of prolonged attention by males. Ad libitum sampling was used to record all observed mount attempts, mounts, and copulations performed by males.

Data analysis.—A Wilcoxon matched-pairs test was used to compare the distance to receptive females for males that simultaneously attended the same female but displayed different mating tactics (Sheskin 2004). Because attended females were scanned multiple times per day (resulting in multiple male–female distances for the same pair of animals), mean values per female and day were used for this test.

To examine differences in the activity budgets of individual males as a function of age and the mating tactic adopted, mixed-effects models using restricted maximum-likelihood method were employed, with animal identification and year of observation as random factors and mating tactic and age as fixed effects (Crawley 2007). To investigate the relationship between age of an individual male and mating tactic, the proportion of time a male spent in the different mating tactics was calculated. Restricted maximum-likelihood mixed-effects models were then fitted with age as a fixed effect and animal identification and year of observation as random effects. For all of these analyses, only focal observations lasting >30 min were used. Before analyses, the proportion of time males spent in each activity or tactic was arcsine square-root transformed to approximate a normal distribution (Zar 1999). Residuals for the restricted maximum-likelihood models were normally distributed.

Binomial tests were conducted to examine differences in the number of mounts and copulations by males that adopted different mating tactics (Sheskin 2004). To explore the effect of the age of males on the frequency of each mating tactic, we compared the ages and mating tactics of males associated with

TABLE 1.—Numbers (mean \pm SD; maximum) and sex ratios (mean \pm SD) of Alpine ibex (*Capra ibex ibex*) in the study area. Data are from censuses conducted during the rutting seasons in 2005–2006, 2006–2007, and 2007–2008.

Year	No. censuses	Females	Males	Juveniles	Total	Sex ratio (males/females)
2005–2006 ^a	38	29.1 \pm 7.8; 40	17.3 \pm 6.0; 29	11.2 \pm 3.4; 17	57.6 \pm 14.5; 78	0.62 \pm 0.19
2006–2007 ^b	13	89.6 \pm 10.9; 111	67.8 \pm 9.5; 81	36.6 \pm 3.8; 42	194.8 \pm 21.2; 221	0.76 \pm 0.10
2007–2008 ^b	5	109.4 \pm 9.6; 120	84.4 \pm 6.5; 95	61.0 \pm 2.5; 63	255 \pm 13.23; 266	0.77 \pm 0.09

^a Only a part of the population was monitored.

^b Entire population was monitored. Because of the size of the study area, censuses were spread over 2 consecutive days with safe snow conditions, contributing to the small sample sizes.

attended females. Because these females were scanned multiple times per day, only the 1st observation per day per female was used to avoid pseudoreplication. Frequency distributions of the observed mating tactics were calculated for each age class (year) of males and generalized additive models with Poisson errors were used to assess potential behavioral differences between age classes (Crawley 2007).

To account for the possibility that age-dependent frequency distributions were influenced by the number of males present in the different age classes (i.e., by the male age structure of the population each year), we calculated a standardized tactic index (S_i), which represented the average contribution of an individual of a specific age class i to the frequency of different mating tactics. This was done using the formula:

$$S_i = O_i / \left[N_{ix} \sum (O_i / N_i) \right],$$

where O_i is the observed frequency of the tactic in the age class i and N_i is the average number of males in the age class i present during that season. The standardized values S_i of the different age classes i were then averaged over the 3 years of the study. Generalized additive models were used to test for age effects on the resulting averaged standardized values (Crawley 2007).

RESULTS

Population size and structure.—Censuses of animal numbers during the rutting seasons in 2006–2007 and 2007–2008 indicated that population size varied between 220 and 270 animals, with an adult (age ≥ 1 year) sex ratio of 0.62–0.77 males per female (Table 1). The number of males per age class showed a general trend to decline with increasing age (Fig. 1); oldest males aged 12, 13, and 14 years in the 3 seasons, respectively.

Spatial and temporal distribution of receptive females.—During all 3 years of the study, female Alpine ibex showed a patchy spatial distribution during the rutting season, with females distributed in small aggregations containing 1–20 individuals (Fig. 2). Distances between aggregations were typically less than a few hundred meters, permitting individual males to move between adjacent groups of females within a few minutes.

A total of 211 females were observed that were attended by multiple males during the study. The dates on which the 1st female associations were recorded were 9, 5, and 13 December in 2005, 2006, and 2007, respectively. During the rut in 2005–2006, observations were spread over 48 days; 69.8% of observed

mating associations occurred in the first 2 weeks after the beginning of the rut, with 86.7% and 98.1% of mating associations completed by weeks 4 and 5, respectively. The frequency of associations peaked during week 2, when 43.3% of all associations were observed. The same general pattern was observed in the 2 subsequent years, when observations continued for 38 and 29 days after the beginning of the rut.

Daily scans of male–female associations indicated that female alpine ibex were of interest to males for only a brief period of time. Thus, only 4 (15%) of 27 individually identifiable females were in association with males for ≥ 2 consecutive days. Five identifiable females were observed associating with males at 2 different times within a single rutting period; the intervals between successive associations by these females were 18 and 21 days, suggesting that these females may have undergone 2 rounds of sexual receptivity.

Qualitative description of observed mating tactics.—Our observations confirmed that during the rut, male Alpine ibex adopted 2 different mating tactics to gain access to receptive

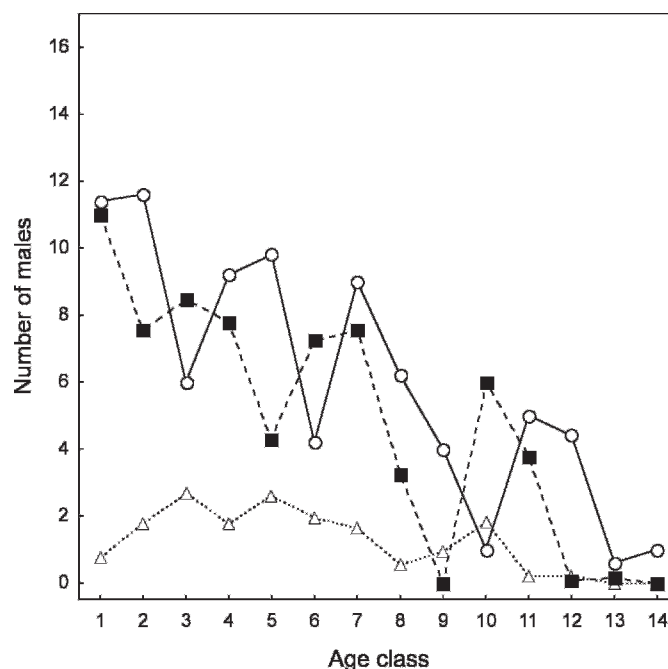


FIG. 1.—Mean age structure of male Alpine ibex (*Capra ibex ibex*) in the study area during the rutting periods in 2005–2006 (open triangles), 2006–2007 (filled squares), and 2007–2008 (open circles), respectively. In 2005–2006, only a part of the study population was monitored.

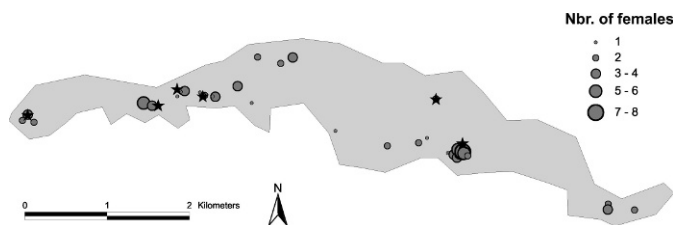


FIG. 2.—Sample spatial distribution of adult female Alpine ibex (*Capra ibex ibex*) on the study site during the rutting period. Data are from animal censuses performed on 20 and 21 December in 2006. The size of each circle denotes the number of females in that aggregation; stars indicate groups containing a receptive female during the censuses.

females: one tactic, called tending, was adopted by apparently dominant males, whereas the other tactic, called coursing, was adopted by apparently subordinate males. Tending males consistently followed individual females with which they were associated and which they courted intensively. Typically, a tending male had exclusive access to a female (Fig. 3) and would defend her against competitors, usually via short displacements, if other males attempted to approach the female. In contrast, coursing males did not have free access to receptive females. Only if a physical obstacle separated the tending and the coursing male did the latter approach the female without being immediately displaced. Normally, however, coursing males remained several meters distant from the female and her tending male (Fig. 3). When the female started to run, all associated males (tending and coursing) ran after her (Fig. 4), with the coursing males trying to bypass the tending male to mount the female, often while running (see below). Coursing males were never observed to initiate such chases. That is, they never drove the female away from the tending male as long as the female and tending male were standing close together nor did they attempt to engage the tending male in a fight. Instead, coursing males always waited for the female to move or run away from the tending



FIG. 3.—A female Alpine ibex (*Capra ibex ibex*; lying on rock) being tended by 1 male (next to female), with 3 other coursing males in close proximity (foreground). Photo by C. S. Willisich.



FIG. 4.—Five male Alpine ibex (*Capra ibex ibex*) pursuing a receptive female. The female is the animal farthest to the right. The tending male is the animal farthest to the left. The remaining animals are coursing males; these males often attempt to mount females during such chases. Photo by I. Glanzmann.

male before engaging in pursuit. These tactics were not fixed and individual males were seen to switch between tending and coursing both within and between seasons.

Number and spatial distribution of associated males.—No more than 1 male was observed to tend a female at a given point in time. The number of coursing males per female ranged from 1 to 10, with a median of 3.0 males per female (interquartile range: 2.0–3.75). Tending males were typically located significantly closer (1.16 female body lengths) to females than the nearest coursing male (5.0 female body lengths; interquartile ranges: 0.83–2.00 and 3.50–7.0, respectively; $n = 197$, $Z = 11.91$, $P < 0.0001$).

Activity budgets while tending and coursing.—During the 3 annual rutting periods, a total of 786 h of focal observations were completed on 57 different males; the mean (\pm SD) duration of each focal observation session was 5.0 ± 2.0 h, yielding a mean of 13.8 ± 11.3 h of observation per focal animal. The restricted maximum-likelihood mixed-effects model showed that, when coursing, males allocated an overall greater percentage of their time to low-cost behaviors (i.e., feeding, standing, and lying) than they did when they were tending ($85.4\% \pm 11.6\%$ versus $52.1\% \pm 28.9\%$). In contrast, the overall percentage of time spent in high-cost behaviors (i.e., courtship, agonistic behaviors, and moving) was greater while tending than while coursing ($45.1\% \pm 29.9\%$ versus $14.3\% \pm 11.7\%$). Age had no significant effect on the percentage of time allocated to either of these categories of behavior (Table 2).

Mounts and copulations.—A total of 81 mounts (including 24 copulations) were recorded for the 211 females tended during this study. Thirty-one of these mounts involved a single female who was the recipient of 27 mounts by at least 7 different males within a period of 19 min. The behavior of this female, specifically her slow movements and lack of effort to escape approaching males, suggested that she was injured and

TABLE 2.—Effects of age and tactic (coursing and tending) on the proportion of time that male Alpine ibex (*Capra ibex ibex*) spent in low-cost and high-cost behavior as a function of the mating tactic adopted. Restricted maximum-likelihood mixed-effects model: Behavior \sim Tactic + Age + Animal identification + Season. Intercepts and random effects Animal identification and Season are not shown.

	Factor	Effect size	SE	df.	t-value	P-value
Low-cost behavior	Age	0.017	0.012	52	1.42	>0.1
	Tactic	0.429	0.057	53	7.57	<0.001
High-cost behavior	Age	-0.020	0.012	52	-1.68	<0.1
	Tactic	-0.410	0.058	53	-7.04	<0.001

thus we excluded this female from all subsequent analyses of mounting and copulation behavior.

Of the remaining 210 females, 13 were seen to engage in copulations; 20 of these copulations were with tending males, whereas 4 were with coursing males ($n_{\text{tend}} = 20$, $n_{\text{course}} = 4$; binomial test, $P = 0.002$). None of these females copulated with >1 male. On average, each female engaged in 1.7 ± 1.0 copulations. Of the 50 mounts recorded (involving 21 different females), 30 were by tending males, whereas 20 were by coursing males ($n_{\text{tend}} = 30$, $n_{\text{course}} = 20$; binomial test, $P = 0.203$). Two females were mounted by 3 different males, whereas 5 were mounted by 2 different males; all of the remaining females were mounted by only a single male. On average, each female engaged in 2.3 ± 1.4 mounts.

Analysis of 144 h of continuous focal observations on 32 tended females (4.2 ± 2.5 h per tended female) monitored during 2005–2006 indicated that females received 0.22 mounts and 0.05 copulations/h while being tended. During the same focal observations, 102 instances were recorded in which a female ran in front of (i.e., was pursued by) the males for at least 5 s, which corresponds to 0.7 runs/h while being tended. On 18 occasions during these runs, males attempted to mount the female; these attempts resulted in 11 mounts. Thus, tended females received 0.18 mount attempts and 0.11 mounts per run. All observed mount attempts and mounts recorded during runs were performed by coursing males. Tending males never tried to mount a female during a run; this difference between tending and coursing males was significant (mount attempts: $n_{\text{tend}} = 0$, $n_{\text{course}} = 18$; binomial test, $P < 0.0001$). Coursing males conducted 11 (79%) of their 14 total observed mounts during runs; the other 3 mounts occurred when the

TABLE 3.—Effect of age on the proportion of time spent tending and coursing by male Alpine ibex (*Capra ibex ibex*). Restricted maximum-likelihood mixed-effects model: Tactic \sim Age + Animal identification + Season. Random effects Animal identification and Season are not shown.

	Factor	Effect size	SE	df.	t-value	P-value
Tending	Intercept	-0.074	0.163	59	-0.45	0.65
	Age	0.049	0.016	59	3.14	<0.01
Coursing	Intercept	0.809	0.124	59	6.50	<0.001
	Age	-0.066	0.016	59	-4.12	<0.001

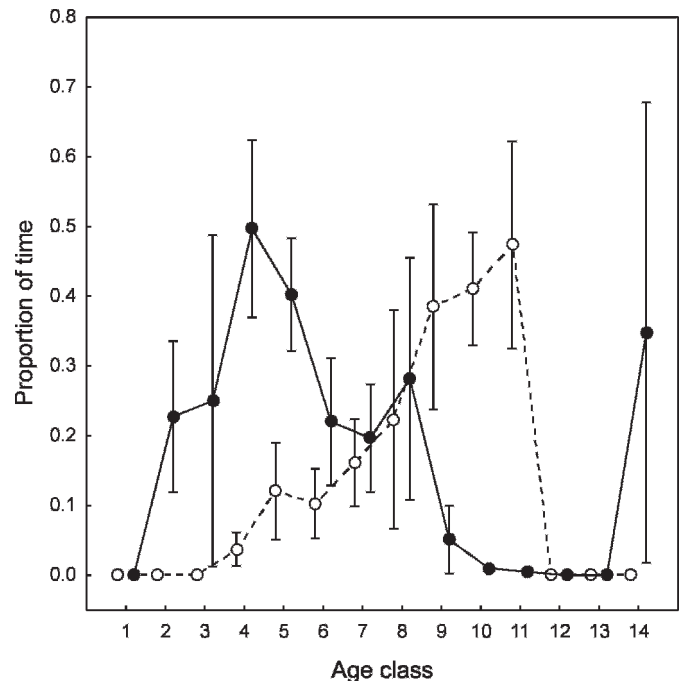


FIG. 5.—Mean (\pm SE) proportion of time that male Alpine ibex (*Capra ibex ibex*) spent tending (open circles, dashed line) versus coursing (filled circles, solid line) as a function of age class.

female was standing still, but at a relatively large distance from the tending male.

Age-dependent adoption of mating tactics.—Age had a considerable effect on the mating tactic adopted by individual males during the first 4 weeks of the rut, when the majority of instances of tending females were recorded. The restricted maximum-likelihood mixed-effects model showed that the proportion of time spent coursing decreased with increasing age of males (Table 3). However, closer inspection of the data revealed that the proportion of time spent coursing increased until the age of 4 years; only after that age did the proportion of time spent coursing decline (Fig. 5). Males aged 10–13 years devoted only small proportion of their time to this tactic. The apparent increase in coursing for age class 14 years was due to a single male that spent a large proportion of time coursing during 1 day of observation. In comparison, the percentage of time spent tending increased significantly with the age of males (Table 3). Males ≤ 4 years devoted almost no time to the tending tactic. The proportion of time spent tending peaked between 9 and 11 years of age, whereas a marked decrease became apparent thereafter (Fig. 5).

At the population level, generalized additive models demonstrated that the frequencies with which the tending and coursing tactics were observed varied significantly with the age of males (tending \sim s(Age): $df. = 6.9$, $\chi^2 = 77.4$, $P > 0.0001$; coursing \sim s(Age): $df. = 7.7$, $\chi^2 = 297.8$, $P > 0.0001$; Fig. 6). Coursing was displayed primarily by males ≤ 7 years of age; collectively, these animals accounted for 90% of all observations of coursing. Conversely, males ≥ 7 years accounted for about 95.7% of all observed episodes of tending. Among the older males, the age classes 10 and 11 years accounted for 57.8% of the observed

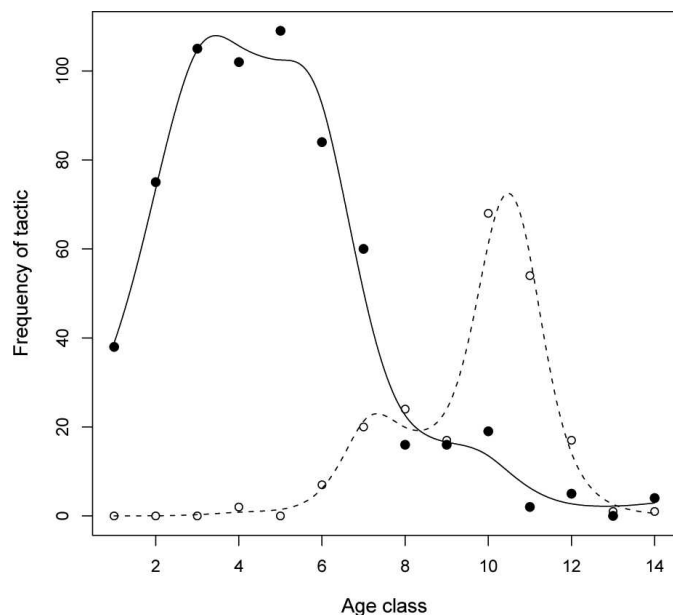


FIG. 6.—Frequency distributions of the observed tending (open circles, dashed line) and coursing male (filled circles, solid line) Alpine ibex as a function of age class. Lines are fitted smooth curves predicted by the generalized additive models (for details see text).

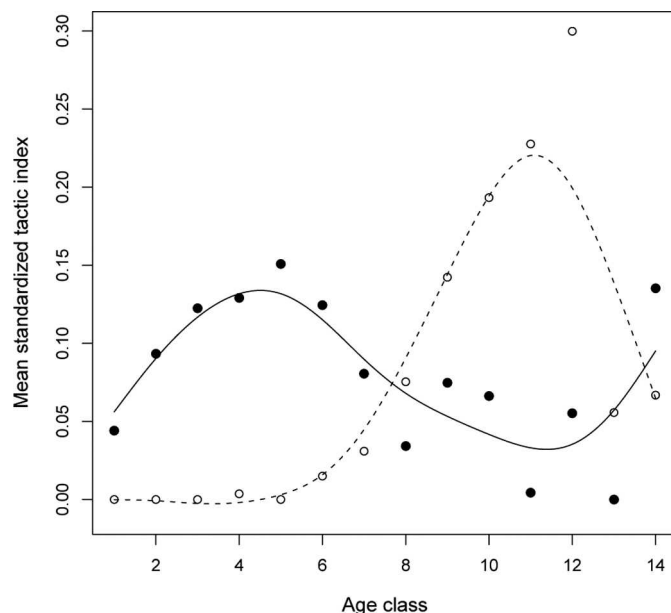


FIG. 7.—Mean standardized tending (open circles, dashed line) and coursing (filled circles, solid line) indices as a function of the age class. Lines are fitted smooth curves predicted by the generalized additive models (for details see text).

tending events, whereas males ≥ 12 years represented only 9.0% of tending episodes.

The effects of age on the observed mating tactics remained significant when the number of males per age class was taken into account (standardized tending index $\sim s(\text{Age})$: estimated $d.f. = 4.4$, $F = 10.0$, $P = 0.002$; standardized coursing index $\sim s(\text{Age})$: estimated $d.f. = 4.2$, $F = 3.7$, $P = 0.044$). Hence, the standardized index for the tending tactic was very low for all age classes ≤ 6 years (Fig. 7). A steady increase could be detected for age classes of 7–12 years of age, with a marked decline thereafter. However, the standardized coursing index was highest for age classes of 3–6 years and lowest for age classes of 8–13 years. Collectively, these findings suggest that male reproductive tactics are strongly influenced by the age of males.

DISCUSSION

As in other seasonally breeding ungulates inhabiting alpine environments (e.g., red deer [Clutton-Brock et al. 1982] and Alpine chamois [Willisch and Ingold 2007]), mating activity in Alpine ibex was spread over >4 weeks per year. Receptive females were only moderately temporally synchronized and showed a patchy spatial distribution in the study area, leading to a high level of intramale competition for access to mates. The 2 alternative male mating tactics documented in the study population—tending and coursing—bear a strong resemblance to mating tactics previously reported for bighorn sheep (Hogg 1984, 1987), mountain goats (*Oreamnos americanus*—Mainguy et al. 2008), and feral goats (*Capra hircus*—Saunders et al. 2005). Our observations indicate that both tactics resulted in mating opportunities, although mating success in the form of copulations was higher for the tending tactic. In our study

population, the adoption of alternative mating tactics was strongly age-dependent, similar to findings for other polygynous ungulates with alternative mating tactics (Mainguy et al. 2008; Saunders et al. 2005). Tending was most common among older males, whereas coursing was most pronounced in younger males. Interestingly, regardless of age, the proportion of time that individual males spent in low-cost behaviors (i.e., feeding, standing, and lying) was greater for coursing than for tending, whereas the opposite was true for high-cost behaviors (i.e., moving and social behaviors).

Considering the spatial and temporal distribution of receptive females in the population in this study, the high level of intramale competition, and the presumably strong sexual selection associated with these conditions (Shuster and Wade 2003), it is not surprising that males in the population engaged in alternative mating tactics. The finding that individual male Alpine ibex of all ages switched between tactics within the same rutting period is in accordance with other species with similar mating systems (e.g., bighorn sheep [Hogg 1987] and feral goats [Saunders et al. 2005]) and suggests that these tactics represent a behavioral polyphenism within Alpine ibex. In contrast to other mating phenotypes (i.e., developmental or genetic polymorphisms), behavioral polyphenisms are characterized by frequent and rapid reversibility (Shuster and Wade 2003). As a result, individual males have the potential to respond quickly to changing mating conditions to maximize their reproductive success.

At the same time, however, our study demonstrated that age had a strong effect on which mating tactic an individual male adopted. This was evident not only at the individual level (proportion of time individuals spent in each tactic), but also at the level of the population (overall frequency with which each

tactic occurred). Accordingly, tending was adopted primarily by older males aged 9–12 years. Coursing, on the other hand, was adopted mainly by males ranging from 2 to 6–7 years of age. These patterns are in general consistent with data from other polygynous ungulates in which mating tactics are size- or weight-dependent, or both, and therefore also age-dependent (Isvaran 2005; Wolff 2008). To establish and maintain access to receptive females by tending, usually high dominance status (see also Hogg 1984; Mainguy et al. 2008; Saunders et al. 2005) and therefore a generally large body size is required (Decristophoris et al. 2007). Because body size in male Alpine ibex increases steadily with age up to about 8–9 years (Lüps et al. 2007), it is reasonable to assume that only older, fully grown males are able to apply the tending tactic successfully. In contrast, agility and running speed are likely to be the crucial qualities of successful coursing males (Coltman et al. 2002; Hogg and Forbes 1997), because these animals must catch up with running females to copulate. Agility in male Alpine ibex is likely to be negatively weight- and size-dependent and, hence, coursing in this species (as in other polygynous ungulates with comparable mating tactics—Hogg and Forbes 1997; Saunders et al. 2005) should be more common among younger males. Interestingly, the average standardized tending indices (which estimated the contribution to the recorded tending events while taking into account the number of males per age class) for the 2 oldest age classes (13 and 14 years) were noticeably reduced compared to the slightly younger age classes, suggesting that these males might have passed their peak of reproductive performance and were showing signs of senescence.

Although coursing males did not have free access to receptive females, they were capable of making use of sudden mating opportunities, as shown by the observed coursing mounts and copulations. To succeed, coursing male Alpine ibex had to rely on the behavior of the female; these males did not try to create mating opportunities but instead waited for the female to move or run away from the tending male. Coursing males in other species, such as bighorn sheep and feral goats, are known to actively initiate chases of receptive females either by overt aggression against the tending male or by driving away the female (Hogg 1984; Saunders et al. 2005). In comparison, coursing male Alpine ibex were relatively passive and made only opportunistic use of mating opportunities that arose as a result of female behavior. This less active role in coursing may help to explain the relatively low rates of mounts and copulations detected during this study. Receptive females in the study population engaged in on average only 0.05 copulations/h tended; in contrast, female bighorn sheep (in which males take a more active role in initiating coursing) engage in 1–2.5 copulations/h (data derived from Hogg and Forbes [1997]). According to Hogg (1988), individual female bighorn sheep experienced up to 60 copulations during 1 estrous period; in contrast, individual female Alpine ibex engaged in an average of <2 copulations per estrous period.

Our behavioral observations strongly suggest that both mating tactics displayed by male Alpine ibex may lead to mating success, although only about 1 in 6 copulations was

performed by coursing males. In contrast, the number of copulations by coursing male bighorn sheep, which are known to sire >40% of the lambs (Hogg and Forbes 1997), was nearly equal to the number achieved by tending males (Hogg 1988). Whether coursing Alpine ibex can attain levels of reproductive success similar to those for coursing male bighorn (Hogg and Forbes 1997) or Soay sheep (*Ovis aries*—Coltman et al. 1999) remains unknown. Although the low proportion of copulations observed for coursing male Alpine ibex suggests that this is unlikely, genetic analyses of paternity are required to determine actual reproductive success of coursing versus tending males in this species.

Assuming that spending more time in energy-consuming behaviors contributes negatively to the energy balance of animals (Pelletier 2005; Willisch and Ingold 2007), our analyses of time budgets suggest that coursing is energetically less expensive than tending and that the energetic difference between these tactics may be particularly pronounced in Alpine ibex. Accordingly, while coursing male Alpine ibex allocated on average 84.5% of their time to so-called low-cost behaviors and only 14.3% to high-cost behaviors. In comparison, coursing male bighorn sheep spent only about 61% of their time in low-cost behaviors, whereas the high-cost behaviors accounted for a remarkable 37% (data derived from Pelletier [2005]). Because mortality of male ungulates inhabiting temperate climates is thought to depend greatly on rut-related investments in reproduction (Toïgo and Gaillard 2003) the adoption of low-cost tactics is expected to enhance the survival of their users. Hence, male Alpine ibex engaging in coursing are likely to enjoy high survival without foregoing the possibility of participating in reproduction. As predicted, the age-dependent adoption of the opportunistic low-cost tactic coursing could, therefore, contribute to the consistently high survival found among male Alpine ibex up to 8 years of age.

On the other hand, given that coursing was only rarely adopted by males ≥ 9 years of age, the high survival rates of about 85–96% (depending on the ecological conditions) among 8- to 13-year-old males cannot directly be attributed to the low-cost tactic coursing. Neither can they be explained by an energetically favorable tending tactic, because this tactic appears to incur high energetic costs in male Alpine ibex. Accordingly, only 45.1% of the tending time was devoted to low-cost behaviors, whereas time spent in high-cost behaviors constituted 52.1%. Tending male bighorn sheep, in comparison, spent about 78% of their time in low-cost behaviors and correspondingly much less time (about 22%) in high-cost behaviors (data derived from Pelletier [2005]), suggesting that the costs of tending are higher in Alpine ibex. Still, yearly survival for male bighorn sheep did not exceed 80% when they reached their peak in breeding activity at 5–8 years of age (Bonenfant et al. 2009).

Considering that the environment-related decline in survival detected by Toïgo et al. (2007) involved largely the same age classes that participated most actively in rutting and that made most extensive use of the tending tactic, our results suggest that rut-related behavior, nevertheless, plays an important role

in the survival and energetics of Alpine ibex. Another possible mechanism adding to the good survival of older males might therefore be reduction of energy-intensive intramale competitions as a secondary effect of the passive and less overt behavior of coursing males. Because tending males have to defend receptive females against multiple coursing competitors, they might particularly profit from the fact that coursing males do not use overt aggression to attain temporary access to defended females. As a consequence, tending male Alpine ibex might be able to cut down on costly interactions, because they need not continuously block attacks by coursing males. Compared to other polygynous species in which frequency and intensity of intramale competitions are known to culminate concomitantly with the peak in mating activity (Clutton-Brock et al. 1979), tending male Alpine ibex might experience considerable energy savings that could ultimately lead to an improved rate of survival.

Overall, our study demonstrated that the comparatively high survival reported previously for adult male Alpine ibex may result at least partially from the specific alternative mating tactics employed by males during the rutting season. In contrast to tending, coursing appeared to be a low-cost tactic that may directly contribute to the relatively good survival of younger males, which are the principal users of this tactic. Further, our observations indicate that the passive nature of coursing in this species might also confer survival benefits to older, tending males by reducing the costs associated with defending females from reproductive competitors. Future studies that directly quantify the energetic consequences of mating behavior in Alpine ibex will be valuable in demonstrating the impacts of alternative male mating tactics on the life-history patterns of these animals.

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