

# Dirty ptarmigan: behavioral modification of conspicuous male plumage

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Males of many bird species acquire a conspicuous breeding plumage through molt. Male rock ptarmigan (*Lagopus mutus*), however, become conspicuous in a unique way—as snow melts away from the tundra, their cryptic white winter plumage suddenly becomes exceptionally conspicuous, and remains so for at least 3 weeks. While males remain white, females molt into one of the most cryptic plumages known in birds. From our 17-year field study in arctic North America, we show that, unlike other birds, male rock ptarmigan eventually change from conspicuous to cryptic by soiling their plumage, thereby reducing their conspicuousness six fold before they molt to their cryptic summer plumage. Individual males began to soil their plumage as soon as their mates began egg-laying, and were maximally dirty and relatively cryptic by the time incubation began and their mates no longer fertilizable. Thus male plumage conspicuousness appears to serve a reproductive function. Moreover, both polygynous and bachelor males delayed soiling for a few days after monogamous males, as expected because of the prolonged mating opportunities available to them. We use these data to address a variety of hypotheses to explain both the conspicuousness of breeding males and their subsequent plumage soiling. Given the high predation rate recorded for male ptarmigan during the breeding season, we argue that male conspicuousness is best explained by sexual selection and that plumage soiling is an adaptation that reduces predation risk by increasing camouflage. *Key words*: color, conspicuousness, crypsis, plumage, ptarmigan, sexual selection. [*Behav Ecol* 12:429–438 (2001)]

The explanation of sexual differences in size, weapons, and ornamentation is a cornerstone of Darwin's (1871) theory of sexual selection. In some species such sexual dimorphism occurs year-round (e.g., differences in body size) and might be explained by intersexual differences in foraging, dominance or habitat use (see Andersson, 1994). When the sexes are most dimorphic during the breeding season, sexual selection would seem to be the most compelling explanation. In many species, males (or sometimes females) acquire conspicuous signals like bright colors, distinctive odors, fancy ornaments, or dangerous weapons just before the period of mate attraction and lose them just as rapidly when the breeding season ends, suggesting that these traits are both important for mate acquisition and costly.

Birds provide many of the best examples for which the benefits of conspicuous breeding colors have been documented. In most waterfowl and songbirds, males and females have similar, cryptic plumages in the nonbreeding season but, before the onset of breeding, males molt into a brightly colored plumage while females remain dull-colored. While the influence of sexual selection on such striking dimorphism seems clear (Andersson, 1983; Butcher and Rohwer, 1988), other explanations for this seasonal plumage change have been proposed: bright male plumage might advertise to predators that males are difficult to capture (Baker and Parker, 1979), or might be important in resource holding or species recognition (Butcher and Rohwer, 1988). Only in the past two decades has the pervasive influence of female choice and male–male competition for mates on male plumage traits finally been documented (Andersson, 1994). Thus, the mating ben-

efits of conspicuous male plumage now seem clear but the fact that such plumage is seasonal suggests that there may be associated costs.

The most obvious potential costs of conspicuous plumage are the time and energy required to produce it and an increase in predation risk. While production costs have been difficult to quantify, there is now ample evidence that more conspicuous species suffer greater predation risk (Andersson, 1994). Indeed, comparative studies suggest that interspecific variation in male plumage brightness may be related to mortality costs in both songbirds and waterfowl (Promislow et al., 1992, 1994). Intraspecific variation in conspicuousness has been less well studied and the relation between brightness, conspicuousness, and predation risk within species is still poorly understood (Götmark and Høglfält, 1995).

Rock ptarmigan (*Lagopus mutus*) are the classical case of both conspicuous and cryptic plumage in birds. Darwin (1871), Huxley (1938), and Cott (1940) all discussed these birds as having the most striking case of seasonal change in plumage resulting from the need for camouflage. Rock ptarmigan need to be cryptic because they live year-round on the open tundra where they are particularly vulnerable to predation from falcons and hawks—they comprise 66–100% of the diet of arctic-nesting gyrfalcons (*Falco rusticolus*) during the short, high arctic breeding season (Bergerud, 1988). Moreover, male rock ptarmigan are selectively hunted by gyrfalcons (Cade, 1960; Gardarsson, 1988; Wayne and Jolly, 1958) and male mortality in the breeding season is higher than that of females, being highest in May–June (by gyrfalcons; Cotter et al., 1992; Gardarsson, 1971; Nielsen and Cade, 1990; by hunters; Olpinski, 1986) when they are most conspicuous.

Given this high predation risk, it is surprising that, during the early part of their breeding season (late May to mid-June), male rock ptarmigan are one of the most conspicuous birds known. Both sexes of rock ptarmigan are almost completely white in winter, particularly cryptic against the snow (at least

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to human eyes; Figure 1a), and their plumage does not reflect in the UV-range in a way that would be visible to avian predators and conspicuous against the snow (Montgomerie R, unpublished data). When snow melts in spring, females molt quickly to a mottled brown plumage that makes them cryptic against the tundra (Figure 1b)—one of the best examples of camouflage in vertebrates—while males remain white and thus are highly conspicuous (Figure 1c). Early in the breeding season, females on the tundra are visible to humans at no more than a few meters, whereas males can readily be detected with the naked eye at 1–2 km. It seems clear that female crypticity is an adaptation to reduce predation. Males, too, molt into a cryptic brown plumage in summer but male molt does not begin until well after females have already molted (Holder and Montgomerie, 1993). Why then do males remain conspicuous for so long and how do they deal with the potentially high predation risk of their white plumage early in the breeding season?

In this study, we quantified the patterns of changing conspicuousness of male and female rock ptarmigan in the spring, during 17 years of fieldwork in the North American arctic. We document here an unusual form of plumage modification that helps males mitigate the potentially high costs of conspicuousness—males in all but one of our study populations actively soiled their plumage (Figure 1d), apparently when their conspicuousness no longer served a function. Thus both the process by which male ptarmigan become conspicuous and the behavior that they later use to make their plumage more cryptic are extraordinary. Our analyses of the timing of plumage dirtying suggest that male plumage conspicuousness and dirtiness both serve an adaptive function.

## METHODS

We conducted most of this research from 1981–1993 on 13 km<sup>2</sup> of upland high arctic tundra at Sarcpa Lake, Nunavut, Canada (see Montgomerie et al., 1983 for details). Each year we spent varying periods from 29 May–10 August at this study site, often arriving while ptarmigan were still in late winter flocks and usually staying at least until all females were incubating clutches. Though our research spanned many years, comprehensive data on many aspects of this study were obtained in only 1–2 seasons due to variable weather and working conditions, changing ptarmigan sex ratios, and mating tactics (Brodsky, 1988), a 10-year cycle of population fluctuations of more than an order of magnitude, and the demands of other research. Consequently we often report data from only a single year to illustrate a point, though much more limited data from other years are entirely consistent. All quantitative data presented here are from the Sarcpa Lake population.

At Sarcpa Lake, the snow typically begins to melt in early June and birds of all species begin breeding by the middle of the month. Every year, we monitored ptarmigan population size and mating success, and the distribution and size of male territories. Most ptarmigan were individually color banded in most years. During the first year of our study, we observed that male ptarmigan soiled their immaculate white plumage during the breeding season and we spent the subsequent years gathering data to try to understand why they performed this behavior.

In addition to this long-term study at Sarcpa Lake, we studied rock ptarmigan at seven sites across the Nearctic (Attu Island, Kodiak Island, and Deadhorse, Alaska, Gros Morne, NF, and Ellesmere Island, Bathurst Island, and Igloodik Island, Nunavut) from 1992–1997. At each of these sites, we determined the timing and extent of molt and plumage soiling and recorded behavioral data during the breeding season in the course of other studies (e.g., Holder et al., 1999).

## Plumage characteristics

Throughout June of 1983 and 1987–1989, weather permitting, we monitored daily the molt and plumage status of all male and female ptarmigan on our study site. For each bird we recorded the identity, location, stage of molt (percent of feathers molted, to the nearest 5%), and degree of plumage dirtiness on a 0–4 scale (males only). To standardize dirt scores among years and observers, we used the following criteria: 0 = immaculate or nearly so (Figure 1c) with no more than a few light stains on the belly; 1 = light wash of yellowish or brown visible only at close range (<5 m); 2 = pale gray-brown all over; 3 = distinct dirty streaks on breast and back; 4 = dirty and bedraggled all over, feathers look worn (Figure 1d). Most males were scored from <20 m distance so any slight plumage dirtiness was easily detectable with binoculars. Dirt scores were highly repeatable ( $r_1 = .93$ ; 20 males scored independently by two or more observers within 24 h). Because male dirt scores often alternated between 0 and 1 for a few days when they began to get dirty, we used the last date that they were observed with a score of 0 as an index of the onset of dirtiness.

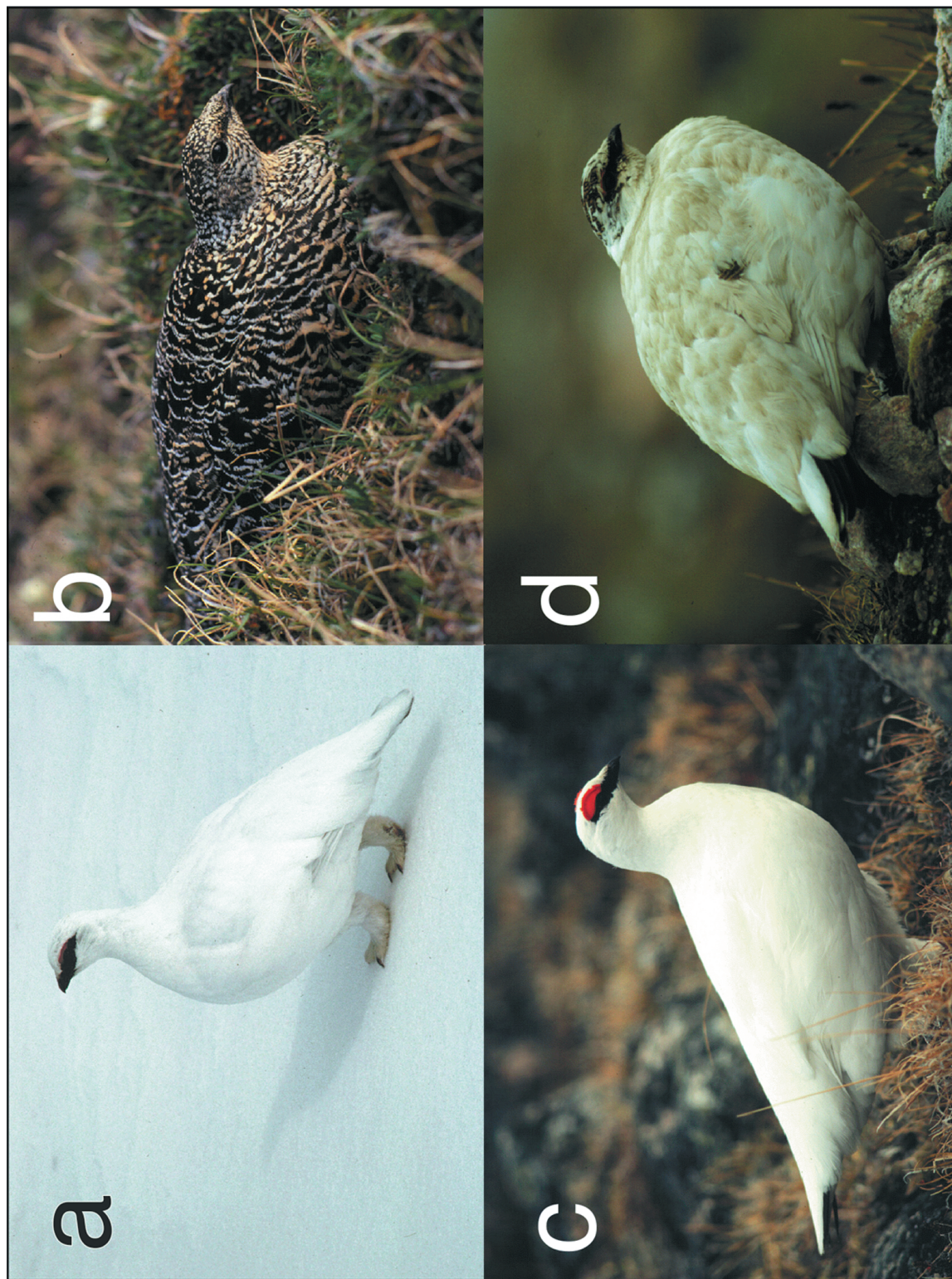
To examine experimentally how plumage dirtiness might influence mate choice we soiled the plumage of three males with a black “indelible” marker in 1987, as soon as they settled on territories. After we darkened their plumage, the plumage color of these males was equivalent to a dirt score of 4 where all other males in the population were scored 0 at the time. Within 2 days all of these males’ plumages were immaculate and a female had settled on each male’s territory. We could not alter male plumage color more permanently without destroying the insulating properties of their feathers, so the experiment was terminated.

## Phenology

To help understand why plumage characteristics of males and females changed, we also quantified snow melt and clutch initiation each year. Snow cover on the whole study area was estimated by eye to the nearest 5% every day. Clutch initiation was determined (1) by direct observation at 2–7 nests each year, (2) by estimation for clutches found during egg-laying or incubation, or (3) by using daily observations of female behavior to estimate the date of clutch initiation of females whose nests were not found. When they begin laying eggs, females are more wary, have almost completed their molt into summer plumage (Figure 1b) and spend little time with their mates. As a result, they are much harder to find (Montgomerie R, Lyon B, and Holder K, personal observations) and their apparent disappearance from their territories, where they are almost always visible before clutch initiation, is an excellent sign that egg-laying has begun (Montgomerie R, unpublished data). To estimate the beginning of egg laying, we assumed that the clutch size was nine, that one egg was laid each day and that the incubation period was 21 days (see Holder and Montgomerie, 1993). Though rock ptarmigan raise only one brood each year, females will lay a second clutch if their first clutch is destroyed during egg-laying or early in the incubation period (Holder and Montgomerie, 1993). We rarely recorded such clutch replacement but we use data only for first clutches here.

## Behavioral characteristics

During time budget observations, we recorded the substrate that the bird was on (sentinel rock, ground, or snow) to determine whether the birds tended to stay on the substrate that best matched their plumage. Sentinel rocks were large boulders (up to 5 m<sup>3</sup>) scattered about the tundra; “ground” refers to snow-free tundra that might be vegetated, stones, gravel, or just bare soil. Time budget data were typically collected in the



**Figure 1** Photographs illustrating rock ptarmigan plumage conspicuousness and crypsis: (a) cryptic male in white winter plumage (Definitive Supplemental; mid-June), (c) conspicuous male in white winter plumage (Definitive Supplemental), later in breeding season (late June), (b) cryptic incubating female in brown summer plumage (Definitive Supplemental; early June), and (d) cryptic male in dirty winter plumage (Definitive Alternate), later in breeding season (late June).

course of other research by watching focal birds for up to several hours at a time and recording the amount of time spent in different activities (e.g., Brodsky, 1988; Brodsky and Montgomerie, 1987).

In 1987–1993, we scanned for ptarmigan by eye during daily censuses across the study area and recorded the distance (to the nearest 10 m) at which a male was first sighted, his dirt score, and his identity (from color bands). Distances were log-transformed to normalize distributions. A similar approach to quantifying conspicuousness, based on the distance that an individual is first detected by eye, has recently been used in a study of reef fishes (Warner and Dill, 2000).

Because it has been suggested that male conspicuousness might deflect predator attention away from the female (Huxley, 1938), we conducted a simple experiment in 1984 on 10 pairs to determine male reaction to the approach of a predator. Humans have probably been a major predator of ptarmigan, at least near human habitation, since humans first settled on tundra regions (see Discussion) but our intention was to use humans as a general predator model as has been done in most studies of nest defense (Montgomerie and Weatherhead, 1988). Whenever a pair was sighted from more than 500 m during the 2-week period before egg-laying began (5–17 June), one of us walked slowly toward the pair while another observer recorded when and how the male moved with respect to the female's location (fly or walk; toward or away from the female). We chose only birds that were clearly paired (i.e., had been seen together often for at least 3 days) and within 50 m of each other when first sighted. We analyzed data from only the first trial on each pair to minimize any effects of habituation.

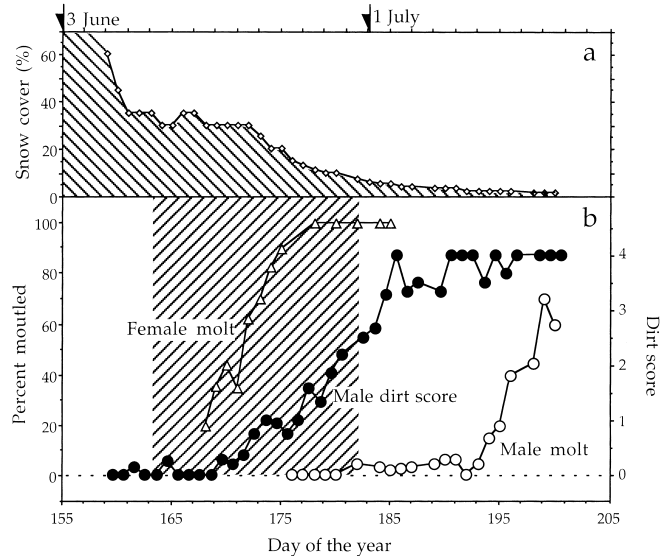
#### Statistical analyses

All variables in analyses of variance (ANOVA) were checked for normality and equality of variances and transformed to meet those assumptions when necessary. We used repeated measures ANOVAs to minimize the effects of pseudoreplication in the analysis of detection distances when marked individuals were sighted more than once, even in different years. Unmarked individuals were all considered to be the same individual in these analyses. In constructing ANOVA models we removed nonsignificant terms from the analyses reported here.

## RESULTS

Conspicuousness and crypsis in rock ptarmigan are influenced by changes in plumage and background (Figure 1), and differ between the sexes in spring due to divergent molting schedules (Figure 2). Thus, males become conspicuous in a unique way—due to a change in background (Figure 1c) rather than a change in plumage. Females molt during the males' courtship and territory establishment phase, where males delay extensive body molt until well after females begin incubation (Figure 2). In a typical year, female molt occurs during snow melt, whereas males delay body molt until the tundra is virtually free of snow (Figure 2).

Despite the delay in molt, male plumage does not remain immaculate. About 10 days after females begin molting, males alter their appearance by increasingly soiling their plumage (Figures 1d and 2), presumably by bathing in dirt and mud. We distinguish this plumage soiling behavior from the usual dust-bathing performed by ptarmigan and many other bird species because dust-bathing is used by birds to clean their plumage (see Discussion). Though we sometimes observed males actively dust-bathing during focal animal time budget studies, they spent very little time at this activity (usually only a few min per day) and never got dirty in the process. Unfor-



**Figure 2**

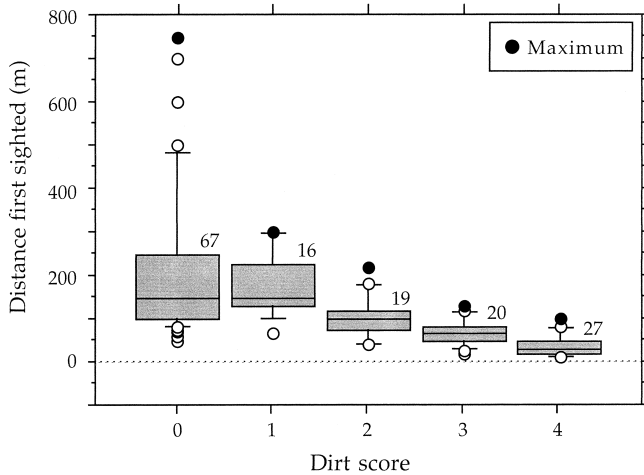
Phenologies of (a) snow cover and (b) female molt ( $n = 22$ ), male plumage soiling ( $n = 16$ ) and male molt ( $n = 16$ ) in spring 1988. Each symbol is the mean for all individuals sampled each day; shaded region in (b) shows the period of egg-laying ( $n = 15$  nests).

tunately, we have never observed a male soiling his plumage in any way and can only assume that they actively bathe in muddy soil.

We observed males with dirty plumage in all years at all study sites except Attu Island (see below), suggesting that male plumage soiling is a general phenomenon in this species, at least in North America (see also MacDonald, 1970; Salomonsen, 1939, for observations of dirty males at other sites). All males in our study population at Sarcpa Lake soiled their plumage before their body molt began in every year of our study.

By soiling their plumage, male ptarmigan greatly reduced their conspicuousness (Figure 1d). The distance that male ptarmigan were visible (i.e., first detected by us) on all substrates decreased significantly as dirtiness increased (repeated measures ANOVA: dirt score,  $F_{4,60} = 27.3$ ,  $p < .0001$ ; Figure 3) with no significant difference among substrates ( $F_{2,70} = 0.68$ ,  $p = .51$ ; score  $\times$  substrate interaction,  $p = .69$ ). To control for the potentially confounding effect of behavior on conspicuousness, we analyzed the 90 observations of 29 males seen foraging on the ground, and found the same pattern ( $F_{4,46} = 26.9$ ,  $p < .0001$ ). Moreover, the maximum distances at which males were first sighted (Figure 3) declined dramatically from 750 m to 300 m when the males first began dirtying their plumage (i.e., changed dirt score from 0 to 1). Mean first-sighting distances (Figure 3) eventually decreased more than 6-fold, from 138 to 22 m (least squares means from ANOVAs).

Given that dirty plumage reduces conspicuousness so dramatically, why do males soil their plumages so late? One possibility is that males cannot soil their plumage until sufficient snow melts to allow them access to dirt, but our data suggest otherwise. In the 8 years for which we observed the entire progress of snow melt, plumage soiling began 1–19 days (mean 9.6 days) after bare patches of ground first appeared (e.g., Figure 2). Thus the delay between the availability of dirt and plumage soiling was highly variable among years, with no significant correlation ( $r = .50$ ,  $p = .20$ ) between the first date of male plumage soiling and the first date that large bare patches of ground were visible (approximately 10% of the



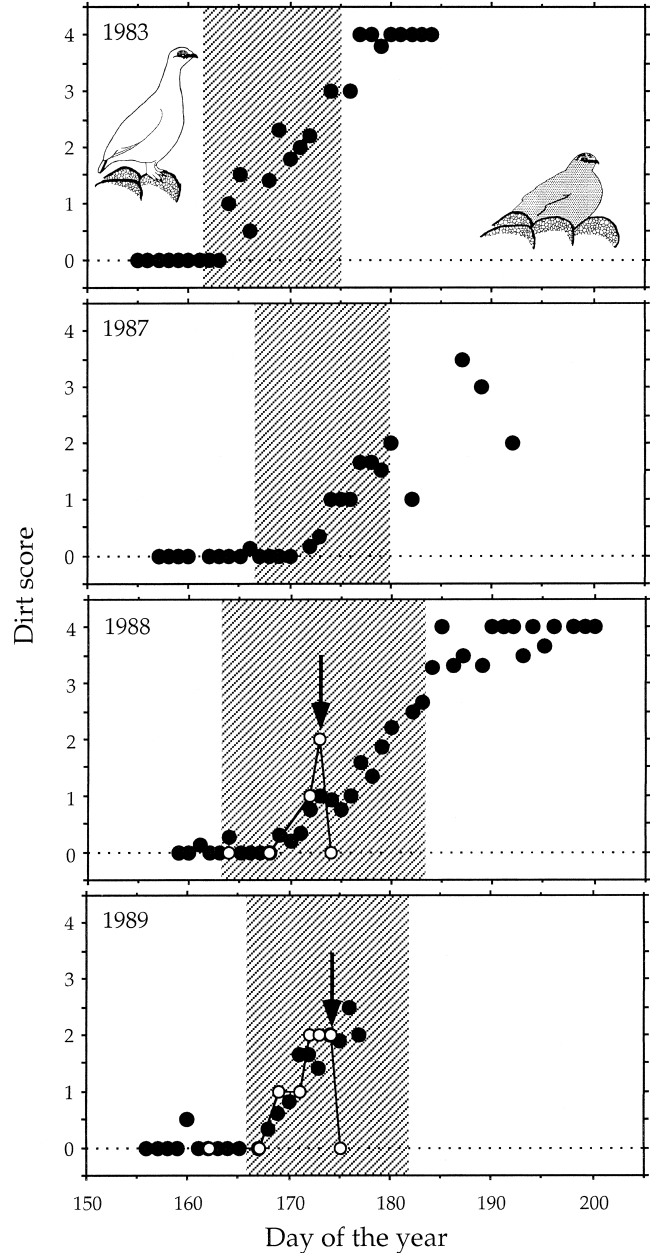
**Figure 3**  
Relation between male plumage dirtiness and conspicuously, measured as the distance males were first sighted by human observers on all substrates. Box plots show 10<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup>, 75<sup>th</sup>, and 90<sup>th</sup> percentiles and all data points outside this range; sample sizes above boxes. Data shown and analyzed were 135 observations of 35 males during 1987–1993 with 1–17 observations per male.

snow had melted). Though the sample size is small and the power of this analysis is low, this result suggests that plumage soiling is not related to the availability of dirt. Moreover, we show below that the timing of plumage soiling is variable among males within years and is much more closely related to the end of the period when females are fertilizable.

Another possibility is that males stay clean and white while females are molting because they spend most of their time on snow patches, where they would be cryptic, during the period of snow melt. However, after the snow began to melt, males with immaculate plumage (score 0) spent almost all of their time (96.4%, range 79–100% for 15 males) on bare ground and rocks, where they were highly conspicuous.

The failure of dirt availability or habitat selection to explain the timing of male dirtiness suggests that males delay dirtying their plumage to obtain some benefit from conspicuous plumage. Indeed, plumage soiling was closely associated with the timing of egg-laying by females. In all 4 years of intensive study (1983, 1987–1989), males began soiling their plumage within 1 or 2 days of females laying their first egg (Figure 4) and were maximally soiled 14–17 days later when clutches were complete and females no longer fertilizable.

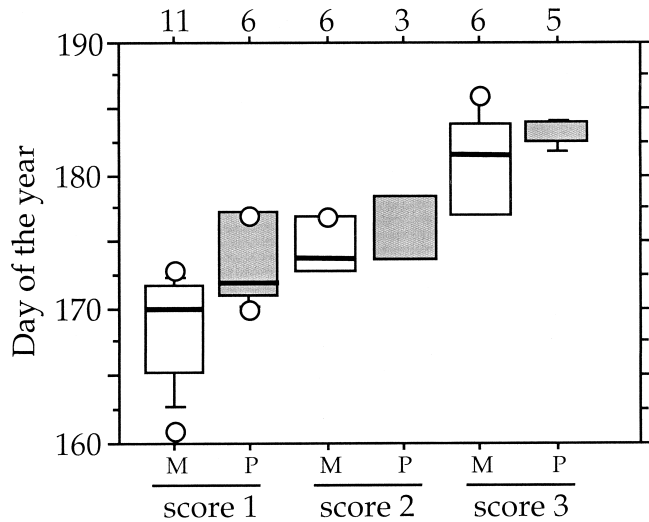
In 1987–1989, the date that each mated male was last seen with a dirt score of 0 was significantly related to ( $r = .62$ ,  $p = .003$ ; analysis of means from 21 males) and, on average, 2.1 days ( $\pm 0.5$  SE) later than the date his mate began egg-laying. To examine year and snow melt effects on this pattern we performed analyses of covariance (ANCOVA) on these data with clutch initiation date as the covariate. The beginning of plumage soiling (last day of score 0) was significantly related to the onset of egg-laying and year of study whether we consider each individual male–female pairing to be independent (ANCOVA: clutch initiation,  $F_{1,25} = 26.5$ ,  $p < .0001$ ; year,  $F_{1,25} = 16.6$ ,  $p = .0004$ ) or analyze mean values for each male across all years (ANCOVA: clutch initiation,  $F_{1,18} = 26.1$ ,  $p < .0001$ ; year,  $F_{1,18} = 12.1$ ,  $p = .003$ ). However the beginning of plumage soiling was not related to the timing of snow melt (analysis of pairs,  $F_{1,25} = 2.9$ ,  $p = .10$ ; analysis of means,  $F_{1,18} = 1.7$ ,  $p = .21$ ). Further support for a causal link between female fertility and male conspicuousness comes from data on two males who immediately cleaned their plumages from me-



**Figure 4**  
Timing of male plumage dirtiness relative to egg-laying in 1983, and 1987–1989. Each dot shows the average dirt score for all males scored that day ( $n = 18, 8, 16, 10$  males, respectively by year). Shading shows the entire egg-laying period each year for females mated to those males and for whom we have accurate estimates of clutch initiation dates ( $n = 4, 6, 15, 8$  nests). Open symbols connected by lines in 1988 and 1989 show changes in dirt scores for two males who cleaned their plumages immediately following predation of their mates' nests (arrows).

dium dirtiness (score 2) to immaculate (score 0) within 24 h of their mates losing their clutches to a predator (Figure 4), and presumably again being fertilizable (as at least one of these females did lay a second clutch).

Data from polygynous and bachelor males provide additional evidence that the onset of plumage dirtying is related to female fertility. (Bachelors are males that were never paired during a given breeding season.) If the timing of dirtying is influenced by sexual selection, polygynous males should soil



**Figure 5** Box plots summarizing the timing of male plumage dirtiness in relation to mating status (M = monogamous, P = polygynous) in 1988. Day 170 was 18 June. Some of the same individual males were recorded at dirt score = 1, 2, and 3. Box plots as in Figure 3; medians indicated by heavier lines.

their plumage later than monogamous males because polygynous males mate sequentially (Brodsky, 1988) and thus have a longer period of female fertility. In 1988, the year for which we had the most data on both polygynous and monogamous males, polygynous males soiled their plumage significantly later than monogamous males (repeated measures ANOVA,  $F_{1,88} = 7.30$ ,  $p = .015$ , Figure 5), on average reaching a dirt score of 2 about 4 days later. Similarly, bachelors should delay plumage soiling since they do not have a partner and thus have extended mating opportunities via extrapair copulations (Brodsky, 1988). In 1983, the year for which we had the most data on bachelor males, the average date that bachelors reached a dirt score of 2 was 2 days later than that for mated males, though the difference was not significant ( $t$  test,  $t = 1.54$ ,  $p = .15$ ,  $n = 6$  mated, 7 bachelor). Thus both bachelor and polygynous males soiled their plumage later than would be expected if dirtying was not related to female fertility (see Discussion).

Finally, our predator deflection experiment yielded results that do not provide strong support for the predator deflection hypothesis. In six of 10 pairs the male flew toward or stayed close to the female, and in four pairs the male flew or walked away. Though the initial response of four males was to move away from the female, three of these males returned within a few minutes and settled close to the female, thereby drawing our attention to the female's location.

## DISCUSSION

We have documented here an apparently unique process by which a male bird acquires a cryptic plumage when his conspicuous plumage no longer serves a reproductive function—by soiling the plumage rather than by molt. This accompanies a unique way, long known to biologists, that male rock ptarmigan become conspicuous in the first place as their habitat changes from white to brown while their plumage remains white. In this study, we quantified this conspicuousness in the field and we document how conspicuousness changes as the males soil their plumage.

Most previous studies of plumage conspicuousness have simply compared pictures of birds and quantified relative con-

spicuousness to the observer on a fairly subjective scale (Baker and Parker, 1979; Promislow et al., 1992, 1994). However, Endler and Théry (1996) measured both the colors and visual backgrounds of three lekking birds in the rainforest and found that the birds' colors and behaviors maximized the amount of visual contrast during their displays. More recently, Andersson et al. (1998) measured the reflectance spectra of both blue tit plumage and the microhabitats visited by the birds and found that reflected light in the UV range contributed significantly to conspicuousness. We have taken a different approach here by quantifying the distance that live birds on the tundra could be detected by human observers. Near human habitation in the arctic, humans are a major predator on ptarmigan (Smith, 1991; Montgomerie R, Lyon B, and Holder K, personal observations) and probably have been as long as humans have inhabited tundra regions. Thus our method of measuring conspicuousness is relevant to the risk of predation by humans. Birds of prey and foxes are also important predators of adult ptarmigan in the breeding season (see below). Immaculate ptarmigan would probably be detectable only at shorter distances by foxes but at much farther distances by raptors, based on their visual acuity compared to humans.

Plumage change by soiling rather than molting offers male ptarmigan the opportunity to become relatively cryptic more quickly, with more flexible timing than molt, and presumably at lower energy cost. Thus, by soiling their plumage, males were able to become relatively cryptic within a few days, as opposed to the 14 days required for females to molt from white to brown plumage (Holder and Montgomerie, 1993). In early July, when there is no more opportunity for breeding, males molt to their brown summer plumage over a 3-week period (Holder and Montgomerie, 1993). Moreover, two males that we studied reversed their crypsis quickly, by cleaning their plumage from dirty to immaculate within 1 day, when their females lost their clutches (and presumably were again fertilizable), a feat that would have been impossible for a molting male. It is not so surprising that this behavior is probably unique among birds because few land birds are white during periods of highest predation risk.

Among birds, a change in the color of existing plumage (rather than a change in color by molt) has been reported in many waterfowl (e.g., snow geese, *Chen caerulescens*) and cranes (e.g., sandhill crane, *Grus canadensis*), in bearded vultures (*Gypaetus barbatus*) and in the red knot (*Calidris canutus*). In waterfowl and cranes the reddish stain on the heads and necks of many individuals is thought to be a passive consequence of foraging in iron-rich water (Höhn, 1955; Kennard, 1918). Bearded vultures, however, actively stain the feathers of their underparts, head and neck by bathing in red soil and the degree of red staining may serve as a status signal in intraspecific encounters (Negro et al., 1999). Red knots also change the color of their plumage at the beginning of the breeding season, as a consequence of a change in the composition of their preening waxes that causes their plumage to become more red when it is preened (Piersma et al., 1999). Most important, plumage redness seems to be a signal used during mate choice in this species (Piersma et al., 1999). Thus plumage coloring in bearded vultures and red knots may serve a cosmetic function whereas in rock ptarmigan the function appears to be camouflage.

Work done elsewhere on predation on ptarmigan during the breeding season indicates that conspicuousness is costly for males. Indeed, gyrfalcons, a major predator of rock ptarmigan, hunt them in a distinctive manner wherein they spot their prey at some distance from a high altitude (200–400 m) then drop low to the ground and approach their quarry less than a few meters over the tundra, where they are less likely

to be detected (White and Weeden, 1966). Ptarmigan mortality rates (due to falcon predation) during the breeding season are exceptionally high and most of that predation is on males, which are more conspicuous than females. In an 18-month study of 31 gyrfalcon territories in Iceland, Nielsen and Cade (1990) found that rock ptarmigan constituted as much as 87% of the prey of these raptors during the breeding season (depending on habitat) and comparable figures have been reported from other regions (Bengston, 1971; Cotter et al., 1992; Gardarsson, 1971, 1988; Langvatn, 1977; Poole and Boag, 1988; Wayne and Jolly, 1958). Most important, Icelandic gyrfalcons preyed mainly on males in white plumage in the spring, up until the time when males stopped defending territories (Nielsen, 1986; Nielsen and Cade, 1990)—just when we observed them beginning to soil their plumage. Over the entire breeding season, Cotter (1991) found that gyrfalcons were responsible for 95% of all predation on rock ptarmigan and that mortality rates in June and July were 50% higher for males (22%) than females (14%). Similarly in Iceland, Gardarsson (1971) found that annual male mortality rates (65%) were higher than those of females (47%) and, in particular, that predation on males during their short (< 2 months) breeding season was extremely high (33%). In that study, gyrfalcons were responsible for all losses by predators and nine territorial males were actually observed being taken by these raptors. It is abundantly clear that breeding male rock ptarmigan suffer one of the highest predation rates ever recorded for birds (e.g., higher than total annual male mortality listed for any species in Promislow et al., 1992, 1994). Thus, we would expect a costly trait like white plumage, that makes a male so conspicuous, to confer significant survival or mating advantages in order to be maintained by natural or sexual selection.

A number of hypotheses can be formulated to explain both the conspicuousness of male rock ptarmigan in spring and their subsequent crypsis resulting from dirty plumage. We discuss each of these below in relation to the evidence that we have presented and data currently available on this species in the literature.

### Hypotheses about plumage conspicuousness

#### *Molting constraint hypotheses*

While female rock ptarmigan molt to become camouflaged, males might remain conspicuous because they are constrained by energy availability or hormones, and not because conspicuous plumage serves an adaptive function. For example, male flight song displays and territory defense are probably energetically costly. Thus one might argue that male ptarmigan delay molt, which is also thought to be energetically costly (Murphy and King, 1992), until after females begin incubating. By waiting until courtship and territorial defense are finished, males could devote more time to foraging and more energy towards the molt.

Salomonsen (1950–1951) also suggested that conspicuous male ptarmigan plumage may not serve an adaptive function but rather may be the result of a hormonal constraint. Since testosterone can act as an inhibitor to molting, Salomonsen argued that males remain conspicuous simply because the spring surge in testosterone coincides with (and triggers) male territoriality and aggression. Thus molting would be inhibited until after testosterone titres subside (see also Stokkan, 1979). An injection of testosterone solution into a single male rock ptarmigan on Bathurst Island, Nunavut, for example, did delay his molt out of white plumage by at least three weeks compared to other males in the population (MacDonald, 1970).

Despite the possibility that hormones and energy may con-

strain male molt, a constraint on molting cannot explain conspicuousness because males can quickly alter their conspicuousness by soiling their plumage, as we have shown, and the timing of such dirtying behavior appears to be quite flexible. Thus, if there were no particular advantage to conspicuousness males should soil their plumage at the same time that females become cryptic by molting.

#### *Soil availability hypothesis*

Although male ptarmigan are able to achieve crypsis by means other than molting, perhaps there are temporal constraints on their ability to soil their plumage. For example, since male rock ptarmigan do not begin to get dirty until 2–4 weeks after the snow begins to melt off the tundra, the timing of male dirtiness may simply be related to the availability of mud or dirt. Though we could not monitor the dirtying properties of the soil on our study areas, the tundra appears to dry out in parallel with the degree of snow melt. As an indirect test of this hypothesis we found no consistency between the average onset of male dirtiness and the timing of snow melt in 8 years of study. Thus in some years the snow was 50% melted by late May where in other years not until mid-June. In all of these years, however, the onset of male dirtiness occurred within 2 days of the beginning of incubation by females, when they were no longer fertilizable. Moreover, the onset of plumage soiling by individual males within years was significantly correlated with the date of clutch initiation by their mate. Thus the maintenance of a conspicuous plumage is more likely to have an adaptive function than simply resulting from factors that constrain a male's ability to soil his plumage.

#### *Background matching hypothesis*

Bright plumage could simply be the result of differential background matching by males and females (Cott, 1940; Endler and Théry, 1996). In many species males and females occupy different microhabitats and even brightly colored males may thus be difficult for predators to see. However, male rock ptarmigan in conspicuous white plumage spent less than 5% of their time on snow, where they would have been more cryptic, even when their territories were still largely snow covered. We reject this background matching hypothesis because males did not preferentially stay on white backgrounds matching their plumage.

#### *Unprofitable prey hypothesis*

Baker and Parker (1979) proposed that bright males might actually advertise to predators that they are better able to escape than are females. This unprofitable prey hypothesis can be rejected because conspicuous male ptarmigan suffer more predation than inconspicuous females (Gardarsson and Moss, 1970; Nielsen, 1986; Nielsen and Cade, 1990) and thus appear to be profitable for avian predators.

#### *Predator deflection hypothesis*

Huxley (1938), referring specifically to ptarmigan, suggested that conspicuous males might deflect predator attention away from females. Our data, however, show that mated males did not consistently deflect the attention of humans away from their females, as this hypothesis would predict. This experiment needs to be repeated with (preferably trained) avian predators since these are the main cause of mortality on breeding male ptarmigan, except near human habitation (Montgomerie R, Lyon B, and Holder K, personal observations).

This hypothesis is also not supported by data from bachelors. Since bachelor males spend so little time in the presence of females (only during attempts to sneak onto other males' territories in pursuit of extrapair copulations; Brodsky, 1988),

an immaculate plumage would serve little or no predator deflection function for those females. Thus, bachelors would be expected to soil their plumage once all females have settled on male territories (and were no longer available for pairing, and predator deflection), at least 10 days before they actually did become dirty. Indeed, bachelors soiled their plumage on average 2 days later than paired males.

#### *Sexual selection hypotheses*

Two lines of evidence, both related to the timing of dirtiness in males, support the idea that the conspicuous male rock ptarmigan plumage has evolved via sexual selection. The strong correlation between the onset of male dirtiness and the date of clutch initiation within pairs suggests that conspicuous male plumage serves a reproductive function either through female preference for immaculate males (mate choice) or through some advantage to immaculate males in territorial defense (male–male competition). Differences in the timing of plumage soiling between monogamous, polygynous and bachelor males also suggest a role for sexual selection in the maintenance of conspicuous plumage. Polygynous males soiled their plumage significantly later than monogamous males as expected if males delay soiling their plumage until their females begin egg-laying (Figure 5). Females settle with polygynous males sequentially (Brodsky, 1988) so second and third females should be fertilizable later than first females and females mated to monogamous males. The mean difference of 4 days between the plumage soiling of monogamous and polygynous males corresponds with our observations of female settling patterns, which show a 2–4 days lag between successive females settling with a given polygynous male (Montgomerie R, unpublished data). Bachelor males also soiled their plumage slightly later than mated males. Since bachelor males roam about seeking copulations with females mated to other males (Brodsky, 1988), such a delay soiling their plumage—until most females in the population were no longer fertilizable (Figures 2 and 4)—would be expected if conspicuousness was important for mate attraction.

If mate choice is the reason that male rock ptarmigan remain conspicuous, why would females prefer to mate with males whose plumage is not molted or soiled? Presumably immaculate plumage signals some aspect of male quality that is useful to females. Since male rock ptarmigan do not participate directly in parental care (Holder and Montgomerie, 1993), it is unlikely that females use male plumage as a signal of parenting ability. However, immaculate male rock ptarmigan may honestly advertise their ability to avoid predation. Low quality males, that for whatever reason (health, poor condition, unwariness) need to become inconspicuous to avoid predation, should therefore fail to obtain a mate. Females could benefit from mating with a high quality male by passing his genes on to her offspring (Andersson, 1994; Zahavi, 1975), by gaining some predator deflection advantage as discussed above, or by obtaining a better territory for food and refuge from harassment by other males seeking extrapair copulations. Mate choice experiments, though difficult in this case, are clearly needed to determine whether females prefer immaculate over soiled males.

Alternatively, male conspicuousness may reduce the energy costs of territorial defense by signaling over long distances and minimizing costly territorial intrusions and chases. Immaculate plumage certainly enhances the effectiveness of the male's plumage as a long-distance signal and thus may reduce intrusion and harassment from neighbors. Thus conspicuousness of territorial males could confer an advantage in male–male interactions, though it is difficult to apply this explanation to bachelors since they did not defend territories.

Interpopulation differences in molt patterns might also be

instructive. Molt data from a large number of populations worldwide (Greenland: Salomonsen, 1939; Svalbard: Steen and Unander, 1985; France: Boudarel, 1988; Russia: Dement'ev and Gladkov, 1967) suggest that male rock ptarmigan typically maintain a conspicuous white plumage in the spring, while females molt to crypsis. Only in Scotland (Watson, 1973) and on the Aleutian Islands, Alaska, USA (Murie, 1959), do males molt at roughly the same time as females. Thus, for example, male rock ptarmigan on Attu Island molt as the snow melts and are never highly conspicuous in spring, even though they are at that time just as active, aggressive, courting and territorial as males in the other populations we have studied (Montgomerie R and Holder K, unpublished data). On Attu, at least, males do not soil their plumage, presumably because plumage soiling would serve no function in making them less conspicuous since they have already molted out of their white winter plumage. If male conspicuousness is due to sexual selection then we would expect plumage conspicuousness (and also plumage soiling) to be absent whenever predation rate is too high for males to bear the cost or too low to make conspicuousness advantageous under sexual selection (Andersson, 1994; Zahavi, 1975). No quantitative data are currently available to test these ideas but our own observations on Attu Island suggest that the predation risk by avian predators there is high.

#### *Time constraint hypothesis*

Correlates of the timing of male plumage change from conspicuous white to a more cryptic dirty plumage provide strong support for a role of sexual selection. However, males defending territories and courting/guarding females might simply not have time to spend soiling their plumage. Thus the relation between the timing of female egg-laying and plumage soiling by males could reflect a time constraint whereby males have more time to soil their plumage after their mate is no longer fertilizable. However, bachelor males soiled their plumage slightly later than mated males even though they did not defend territories and had no female(s) to guard. We have few time budget data on these males because color-banded bachelors were not always easy to locate (since they did not hold territories) but our limited data indicate that they spent only a few min per day time intruding on the territories of mated males (Brodsky and Montgomerie, 1987). While not intruding they foraged and slept and thus apparently had plenty of time to soil their plumage if they could have benefited from the reduced conspicuousness. In addition, our observations that the plumage of territorial males changed from dirty to clean (1) for two males when their females became newly fertilizable due to nest predation and (2) for three other males whose plumage we experimentally soiled suggests that immaculate plumage serves a useful function. In fact those males presumably cleaned their plumage by dust-bathing and preening.

#### **Hypotheses about plumage dirtiness**

Why does male rock ptarmigan plumage become soiled at about the same time as females are no longer sexually receptive?

#### *Nonfunctional hypothesis*

Plumage soiling could conceivably be a nonfunctional side effect of dust bathing. While dust-bathing is common in gallinaceous birds (Johnsgard, 1973), there is no evidence that the plumage of any other species becomes noticeably soiled in the process. Indeed, birds engage in dust-bathing to remove oils and possibly ectoparasites from their plumage and reduce feather damage. The removal of oils thus cleans plum-



age rather than making it dirty (van Liere and Bokma, 1987). Consequently, the soiling of plumage via dust-bathing would itself be unusual in birds and it appears as though male rock ptarmigan actively stain and soil their plumage rather than dust-bathing, as suggested for the plumage staining of bearded vultures (Negro et al., 1999). If we assume that male rock ptarmigan get dirty in the course of normal dust-bathing then both the timing and the degree of plumage dirtiness require explanation.

#### Camouflage hypothesis

It seems clear that plumage dirtiness in male rock ptarmigan serves the adaptive function of camouflage. In this study we have documented that dirty males are indeed more cryptic—at least to human predators—than immaculate males. We also know that breeding male rock ptarmigan suffer one of the highest daily mortality rates known in birds. Further research should be directed at comparing the daily mortality rates of dirty and clean males. Polygynous males might also be expected to suffer higher mortality rates due their prolonged conspicuousness. Assuming that predation risk and conspicuousness are highly correlated, as has been found in comparative studies (Promislow et al., 1992, 1994) and assumed in most work on plumage conspicuousness (e.g., Baker and Parker, 1979), then it is likely that dirty plumage does reduce the risk of predation.

#### Conclusions

Based on the data and arguments presented here, we conclude that the conspicuous plumage of male rock ptarmigan is a product of sexual selection that favors the retention of immaculate (and at the time, cryptic) winter plumage after the snow melts and the birds become highly conspicuous on the tundra. Whether the mechanism of sexual selection is (1) female choice for males who are better able to avoid (honest advertisement hypothesis) or deflect (predator deflection hypothesis) predators, or (2) male–male competition (territory advertisement and defense) is an open question that is best addressed by some critical experiments. For example, it would be most informative to experimentally manipulate male plumages at a site where predation is high (e.g., Iceland, Bengston, 1971; Nielsen and Cade, 1990) and then examine the effects of plumage change on male behavior, predation rates, and female choice. Like many problems in sexual selection, it seems likely that plumage conspicuousness in male rock ptarmigan will have more than one explanation, so the challenge will be to determine the relative importance of different mechanisms in the evolution of this trait.

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