

Variation in male mating behaviour within ungulate populations: patterns and processes

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Intraspecific variation in male mating behaviour is widespread in ungulates. Such variation is particularly dramatic when it takes distinct forms, and these discrete behavioural patterns are called alternative tactics. Alternative male mating tactics in ungulates include female-defence, resource-defence, and lekking. I review patterns and processes in variation in male mating tactics within (as separate from between) ungulate populations. Across ungulates, the greatest diversity of mating tactics is typically shown by lekking populations. Males rarely show irreversible patterns, but often switch between two or more mating tactics. Overall, variation in mating tactics is most likely maintained as a conditional strategy influenced by multiple internal factors (especially age, health, body size) and external factors (particularly density at small, local scales). Much work remains to be done on the costs and benefits associated with different tactics, proximate mechanisms, the role of frequency-dependent selection, and the evolution of female mating behaviour.

Keywords: Intraspecific variation, mating behaviour, alternative tactics, ungulates.

It has long been thought that all individuals of one sex of a species display species-specific behaviour. This 'typological' notion is now known to be false. As with other aspects of phenotype, there is wide variation in behaviour within a species, and often even within a population¹. One aspect of behaviour that shows such extensive variation is mating behaviour. Broad intraspecific variation in mating behaviour is seen in diverse animal taxa including arthropods, fish, amphibians, reptiles, birds and mammals^{1–5}. Among mammals, variation in mating behaviour within populations is particularly common in ungulates^{6–10}. Such intraspecific variation within a population is puzzling because the trait with the highest fitness is expected to drive the other variants to extinction. In this paper, I examine patterns and processes in variation in male mating behaviour within ungulate populations by reviewing results from well-studied species.

I first describe the most frequently observed patterns of variation within ungulate populations. I focus on discrete variation (e.g. female-defence and resource-defence in

the same population) rather than on continuous variation (e.g. variation in the size of resource territories in a population) because discrete differences are arguably the most dramatic form of intraspecific variation. A body of literature which has developed from an interest in discrete variation and which provides a framework for the analysis of such variation is the literature on alternative tactics. I present a brief background on alternative tactics, focusing on the main processes thought to maintain variation in behaviour. I then discuss the relative importance of these processes in maintaining alternative male mating tactics in ungulates.

Patterns of intraspecific variation in ungulates

The two most common ways in which male ungulates attempt to gain matings are by defending females or resources. There are several forms of female-defence. Males may exclusively monopolize relatively stable groups of females (harem-defence: e.g. red deer *Cervus elaphus*¹¹; feral horse *Equus caballus*¹²). Males may try to mate with females in mixed-sex groups containing more than one adult male (female-following: e.g., African buffalo *Syncerus caffer*¹³; fallow deer *Dama dama*¹⁰); this may variously include the temporary defence of oestrus females from other males in the group and the establishment of stable dominance hierarchies. In another form of female-defence, males move over large areas searching for, briefly associating with, and trying to mate with oestrous females (roving: e.g., alpine ibex *Capra ibex*¹⁴). The second common type of male mating tactic is to defend territories containing resources, such as forage, that predictably attract females (resource-based territories: e.g., blackbuck *Antelope cervicapra*^{15–17}, puku *Kobus vardonii*¹⁸). Territorial males attempt to mate with oestrous females as they move through these territories in search of resources. Resource-based territories in ungulates usually cover only a small part of the daily range of females and are largely mating territories¹⁹. Resource-based territories are frequently clustered and vary widely both among and within species in their size, aggregation, and abundance of resources that they contain.

Although the different forms of female- and resource-defence can each occur as the only mating tactic in many ungulate populations, in some, two or more of these tactics may occur together; furthermore, they may be found

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Table 1. Ungulates in which alternative male mating tactics have been studied

| Species | Mating tactics described within a population | Ref. |
|--|--|----------------|
| Bighorn sheep <i>Ovis canadensis</i> | Tending, blocking, coursing | 41 |
| Fringe-eared oryx <i>Oryx gazella</i> | Female-following, resource-based territories | 52 |
| Topi <i>Damaliscus lunatus</i> | i. Female-following, resource-based territories ii. Resource-based territories, satellite territories, lek territories | 22 8, 27 |
| Waterbuck <i>Kobus ellipsiprymnus</i> | Resource-based territories, satellite behaviour, female-following | 20 |
| Uganda kob <i>Kobus kob thomasi</i> | Female-following, solitary territories, lek territories, forced copulation attempts of females on territories by non-territorial males | 40 |
| Kafue lechwe <i>Kobus leche kafuensis</i> | Female-following, solitary territories, lek territories, forced copulation attempts of females on territories by non-territorial males | 21 |
| Black lechwe <i>Kobus leche smithemani</i> | Female-following, resource-based territories | 21 |
| Blackbuck <i>Antelope cervicapra</i> | Female-following, solitary territories, resource-based territories, lek territories, forced copulation attempts of females on territories by non-territorial males | 17, 23, 28 |
| Fallow deer <i>Dama dama</i> | i. Female-following, solitary territories, lek territories, forced copulation attempts of females on territories by non-territorial males, satellite territories (in some populations), resource-based territories (in some populations) ii. Female-following, resource-based territories | 6, 9, 50 53 |
| Red deer <i>Cervus elaphus</i> | i. Harem-defence, sneaking matings ii. Harem-defence, resource-based territories | 11 54 |
| Feral horse <i>Equus caballus</i> | i. Unimale defense of female groups, multimale defense of female groups, sneaking matings ii. Roving, harem-defence, resource-based territories | 55 12 |
| White rhinoceros <i>Ceratotherium simum</i> | Resource-based territories, satellite behaviour | 56 |

even with entirely different kinds of mating behaviour (Table 1). For example, harem-defence is often accompanied with sneaking tactics. Here, not all males attempt to defend groups of females; some may remain close to groups and try to sneak matings with females (e.g., red deer¹¹). Harem-defence has also been observed along with roving behaviour (feral horse *Equus caballus*¹²). Where resource-defence is common, an alternative, satellite behaviour, is sometimes also seen. For example, in the waterbuck *Kobus ellipsiprymnus* some males defend resource territories while others ('satellite males'²⁰) are tolerated within these territories and help defend them but gain very few matings²⁰. In some ungulates, males may show both female-following and resource-based territoriality. For example, in the black lechwe *Kobus leche smithemani*²¹ and in some topi *Damaliscus lunatus*, fallow deer, and blackbuck populations^{7,10,22,23}, some males defend resource-based territories in a part of the range used by females while others attempt to mate with females in mixed-sex herds.

Perhaps the widest range of mating tactics in ungulates occurs in populations of lekking species (Table 1). Lekking is a rare mating behaviour where males defend tiny mating territories in large aggregations. These territories do not contain any obvious resources used by females and females visit the territorial aggregations (leks) solely for mating^{24,25}. In most lekking ungulate populations, only a subset of males hold territories on leks. Other males may

defend solitary territories, defend resource-based territories, try to mate with females in mixed-sex herds, or intrude onto territories and force copulations with females (e.g., Uganda kob *Kobus kob thomasi*²⁶, topi²⁷, fallow deer⁶, blackbuck^{28,29}, Kafue lechwe *Kobus leche kafuensis*²¹).

Discrete (or discontinuous) variation in behaviour: alternative tactics

As in other taxa, such as insects and birds, the most striking behavioural variation within ungulate populations is usually discrete (e.g. males displaying lekking, resource-defence, and female-following within the same population). Because such variation involves more dramatic differences in behaviour and is, thus, more difficult to explain, I focus on discrete variation, rather than on more common continuous variation (e.g., differences among males in the number of females they defend, variation in the size of resource-based territories). Discrete variants of behaviour have been variously termed *alternative tactics*, *variants*, *alternative phenotypes*, etc.^{30–33}. They are thought to be the outcomes of a *strategy*. A strategy is defined as an evolved rule that specifies the allocation of somatic and reproductive effort to alternative tactics^{30,32}. Different decision rules of this kind are termed *alternative strategies*. While a tactic refers to a discrete behaviour pattern, a strategy refers to a decision rule that results in a sequence of dis-

crete behaviour patterns (i.e. a sequence of tactics) that individuals adopt over their life time. Therefore, individuals within a population may follow a single strategy but still display multiple tactics. For example, in some ungulate populations, males typically attempt to sneak matings when young, but switch to defending harems when older¹¹.

Alternative tactics and strategies are the subjects of a large literature (reviewed in refs 3–5, 33). The broad types of patterns in behavioural variation identified are (i) irreversible phenotypes, where individuals adopt a single tactic over their lifetime and population variation is a consequence of differences among individuals in the tactics they adopt, and (ii) reversible phenotypes, where individuals either adopt different tactics sequentially or switch back and forth between tactics; here, population variation is a consequence of variation both within and among individuals⁵. Diverse mechanisms have been proposed to explain these patterns. First, individuals may adopt different tactics based on their condition or status or on environmental cues (condition-dependent or status-dependent or conditional strategy)^{30,33–36}. Second, an individual's behaviour may be constrained by its condition or status (making-the-best-of-a-bad-job strategy)³⁰. Third, alternative phenotypes may be maintained by frequency-dependent selection influencing a genetic polymorphism (alternative strategies)^{32,37}. Frequency-dependent selection may also act on how likely an individual is to display the alternative mating tactics (stochastic mixed strategy)^{32,38}. These processes are not necessarily exclusive and there is increasing evidence that multiple mechanisms probably maintain alternative tactics within a population^{5,33}. These processes are explored in further detail in the next section. Despite over two decades of research, the distinctions between

strategies and tactics, the different kinds of strategies, and the role of genetic and environmental influences in the expression of strategies are still debated^{2,4,5,33,39}. Notwithstanding this controversy, the strong theoretical framework developed in the alternative strategies and tactics literature can be used to examine the processes that maintain behavioural variation within ungulate populations.

What maintains alternative mating tactics within ungulate populations?

Despite the debate in the alternative phenotypes literature, most studies agree that the most common form of phenotypic diversity is a conditional strategy involving alternative tactics^{4,5,33}. Based on internal or external cues, individuals may (i) adopt only one tactic (of many possible tactics) through their lifetime, or (ii) display multiple tactics over their lifetime, either sequentially adopting different tactics or switching back and forth between alternative tactics. Why do we see these alternative tactics? The most general explanation involves variation in the fitness of the alternative phenotypes. If two phenotypes vary along an existing environmental gradient in such a way that there are some points along the gradient where one phenotype has a higher fitness and other points where their relative fitnesses switch, then we expect to see these alternative phenotypes maintained in the population (Figure 1). For example, let us suppose that female densities vary spatially within a population in response to local variation in resources. Let the two mating tactics available to males be to try to mate with females in mixed-sex herds (female-following) or to defend resource-based territories (resource-defence). If the fitness of these two tactics varies with female density (Figure 1), then we would expect males to adopt female-following in areas where densities are low and switch to resource-defence in areas with high female densities. Additionally, variation in male mating tactics may be further favoured by variation among males in the optimal switch point between the two tactics. This optimal switch point can change if other factors influencing the fitness of tactics vary. For example, age often influences the outcome of male–male aggression, with older males more likely to win fights than younger males. If resource-defence carries large aggression costs, then young males may experience greater costs than old males. Therefore, young males may be selected to switch to the more costly tactic at a higher density than old males (Figure 1). Thus, in this example, age together with variation in female densities maintain alternative male mating tactics within a population. Density and age are only two of many factors that may cause fitnesses of alternative mating tactics to vary. What are possible factors that may lead to variation in costs and benefits of alternative male mating tactics and, thus, maintain variation in ungulate populations?

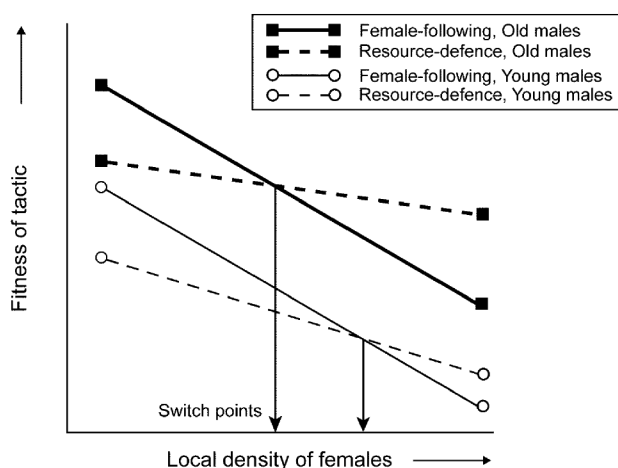


Figure 1. An example of the general process that is likely to maintain alternative male mating tactics within a population. Arrows point to the local density after which males should switch from one optimal tactic to the other. Fitnesses of the two tactics are equal at the switchpoint and, after this point, the fitness difference between the two tactics switches. See text for explanation.

Differences in internal factors among males

Males within a population commonly vary in condition (health, energy reserves). Costs and benefits of alternative mating tactics, and thus the tactic that is optimal, are likely to vary with condition. Therefore, males may be favoured to follow a condition-dependent strategy, an evolved decision-making rule that specified which tactic a male should adopt as his condition changes³³. Alternative phenotypes are then maintained in the population as long as male condition varies. For example, in lekking Uganda kob and blackbuck, males primarily defend territories on leks. This behaviour is costly and males lose condition, at which time they are observed to move to single territories or bachelor herds, feed, and return to leks to display once more to oestrous females (ref. 40, Isvaran unpublished data).

Two similar types of conditional strategies are status- and age-dependent strategies, where males of different status or ages follow different tactics. Subordinate male bighorn sheep attempt to chase and force copulations on oestrous females while dominant males defend females for a large part of their oestrus period⁴¹. Dominant males appear to perform better than subordinate males in direct combat. If subordinate males were to attempt defending females, they would likely suffer the costs of fighting with dominant males but gain few matings because dominant males would outcompete them. Therefore, a better tactic for subordinate males might be to chase females and force matings. Hoggs and Forbes⁴¹ found that up to 40% of lambs in a population may be fathered by males following such harassing tactics. Selection would then act on the status at which males switch from forcing matings to defending females. Such a conditional strategy involves a switch point (age or dominance status) at which the fitnesses of the two tactics are equal. Note that while the fitnesses are equal at a particular age, across the population, the mean fitness of males following one tactic is not necessarily equal to that of males following the other tactic³³.

A different kind of conditional strategy common in ungulates is the making-the-best-of-a-bad-situation strategy. Males in poor condition are likely unable to bear the costs associated with successful mating tactics and they may, thus, be forced to adopt tactics that yield low mating benefits. Several studies suggest that such conditional strategies may be common in ungulates^{9,27}. For example, in the topi, an African antelope, the main mating options available to a male are to defend resource-based territories or territories on leks^{27,42}. Average mating benefits per day are higher for lek territories compared with resource-based territories. This difference is apparently due to a female preference for mating with males on central lek territories⁴³. The costs (fights, injuries, and time spent without feeding) are also high on lek territories and low on resource territories, largely because males compete fiercely for access to territories preferred by females^{27,42}. Bro-Jørgensen and Durant²⁷ found that males on lek terri-

tories were much larger than resource defenders and, therefore, likely better able to defend these high-benefit territories. These findings suggest that alternative mating tactics in topi can be explained by males following a condition-dependent strategy influenced by body size: larger males defend lek territories while smaller males are forced to adopt less-successful resource-defending tactics.

Variation in external conditions

The fitness differences between alternative male mating tactics may change because of spatial and temporal variation in external conditions such as weather, resources, predation, and animal densities. Local density appears to be particularly important in ungulates^{10,25}. Within a population, small-scale spatial variation in density may generate variation in the payoffs (net benefits, taking costs into account) of alternative male mating tactics (density-dependent selection). For example, in lekking blackbuck populations, leks are found in areas of high local female numbers and dispersed territories in areas of low female numbers²⁹. Furthermore, in this study, males appeared to respond to the local distribution of females (local density) rather than to overall population density. Similarly, in fallow deer, males lek in areas of high local female density and show female-following and defence of solitary territories in other areas within the population⁹. Local numbers of females may influence male mating tactics because the number of oestrus females in an area represents the maximum potential mating opportunities available to males in that area; hence, leks may be associated with high local female numbers because costly tactics such as lekking will be favoured only when these costs are offset by high potential benefits.

The effect of female distribution on the payoffs to male mating tactics has also been experimentally demonstrated in a forest population of red deer⁴⁴. Although harem-defence is the most common mating tactic in male red deer, resource-based territoriality has been reported alongside harem-defence in a few Spanish populations. Carranza *et al.*⁴⁴ focused on an area in Spain where male red deer commonly held harems and did not show resource-defence. Resources were typically sparsely distributed in this area, as were females. Carranza *et al.*⁴⁴ experimentally provided clumped resources. They then observed females aggregating at these resource clumps. This was followed by males switching from defending harems to holding territories at these experimental resource sites. Carranza *et al.*⁴⁴ suggest that when females are dispersed, males do better to hold harems, whereas when females are concentrated, resource-defence may yield greater reproductive success than harem-defence.

Apart from spatial variation in density, moderate to high local density in itself may be an important prerequisite for maintaining alternative male mating tactics in un-

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Table 2. Relationship between population density and diversity of alternative male mating tactics within a population in a group of African antelope, *Kobus* spp.

| Species | Density (km ⁻²) | Mating tactics described within a population | Ref. |
|---|-----------------------------|--|--------|
| Red lechwe <i>Kobus leche leche</i> | 7–12 | RT | 57 |
| Puku <i>Kobus vardonii</i> | 35 | RT | 45 |
| Black lechwe <i>Kobus leche smithemani</i> | 134 | RT, FF | 21, 58 |
| Waterbuck <i>Kobus ellipsiprymnus</i> | 70–106 | RT, SB, FF | 20 |
| Kafue lechwe <i>Kobus leche kafuensis</i> | 70–1000 | LT, ST, FM, FF | 59 |
| Uganda kob <i>Kobus kob thomasi</i> | 136 | LT, ST, FM, FF | 40 |

RT – Resource-based territories; FF – Female-following; SB – Satellite behaviour; LT – Lek territories; ST – Solitary territories; FM – Forced mating attempts with females on territories by non-territorial males.

gulates. A survey of a closely related set of African antelope (*Kobus* spp, Table 2) suggests that the number of alternative mating tactics seen in a population is positively related to density. In species at low densities, males defend resource-based territories (e.g. puku⁴⁵). In species at intermediate densities, males may defend resource-based territories, show female-following behaviour or perhaps follow a satellite tactic in the proximity of resource-based territories (e.g., waterbuck²⁰). At high densities, males may lek, defend solitary or resource-based territories, show female-following behaviour, and intrude onto territories to try to force matings on females (e.g., Kafue lechwe²¹). Studies report similar patterns within species. For example, a reduction in kob density was associated with the disappearance of lekking from the repertoire of mating tactics in the population²⁵. In blackbuck, looking across populations, an increase in local female densities was related to an increase in the number of male mating tactics and the frequency of relatively costly tactics (Figure 2). How local density influences the payoffs of alternative mating tactics is still not well understood. A plausible explanation is that increased local female numbers can favour costly tactics by providing greater potential mating benefits and thereby generating greater male–male competition. Furthermore, in some lekking species, females show strong mating preferences. This can further skew the distribution of matings among males so that only a small proportion of males in a population gain matings. Therefore, when costly tactics are favoured and there is a strong mating skew, males at a competitive disadvantage (e.g., males in poor condition, young males) may choose to adopt less costly alternatives, because, for these males, less costly tactics yield greater benefits than more costly alternatives. High local density may, thus, maintain alternative tactics in a population through its influence on maximum potential mating benefits.

External conditions may change not only over space but also over time. Accordingly, payoffs to alternative

mating tactics and, thus, the optimal tactic may show temporal changes. Modelling efforts have shown that a potentially important source of such temporal variation in payoffs is synchrony among females in oestrus^{46,47}. Under conditions of oestrus synchrony, the number of receptive females sharply increases and then decreases. When more females are available, relatively costly tactics may be favoured because high mating benefits can offset the large costs of more competitive tactics. However, as the number of females in oestrus declines, it may pay to switch to less costly tactics. A model of mating tactics in blackbuck predicted that males should defend solitary territories or display to females in mixed-sex groups (both low-cost tactics) when female numbers are low, but switch to lekking (a high-cost tactic) when oestrous female numbers increase⁴⁷. Empirical data suggest that male blackbuck may indeed be sensitive to changing payoffs associated with temporal changes in female numbers²³. For example, in the spring mating peak of 2001, the number of females visiting a lek increased sharply from mid February to mid March and declined thereafter. Corresponding with this, the frequency of males adopting lekking also increased (from 35 to 88 males) and later decreased²³.

Frequency-dependence

It is increasingly recognized that the behaviour of an animal is not only influenced by condition (health, energy reserves) and environmental factors (e.g., resources, predation) but may also be affected by social interactions. The optimal behaviour of an individual will likely depend on the behaviour of other individuals in the population. Game theoretical models have shown that alternative phenotypes may be maintained when the success of a phenotype depends on its frequency in the population^{32,48}. If the fitnesses of two tactics A and B are high when they are rare and low when they are common in the popula-

tion, then any increase in the frequency of A will lead to a reduction in its fitness. The fitness and, consequently, the frequency of B will increase, which in turn will result in a depression in the fitness of B and so on. Many theoretical and empirical studies have focused on such negative frequency-dependence because this simple process is thought to be the most likely to maintain stable frequencies of alternative phenotypes in a population^{5,32,48}. In contrast, other factors, such as the internal and external factors described previously, will maintain alternative phenotypes only as long as they show sufficient variation so that fitness differences between alternative tactics vary.

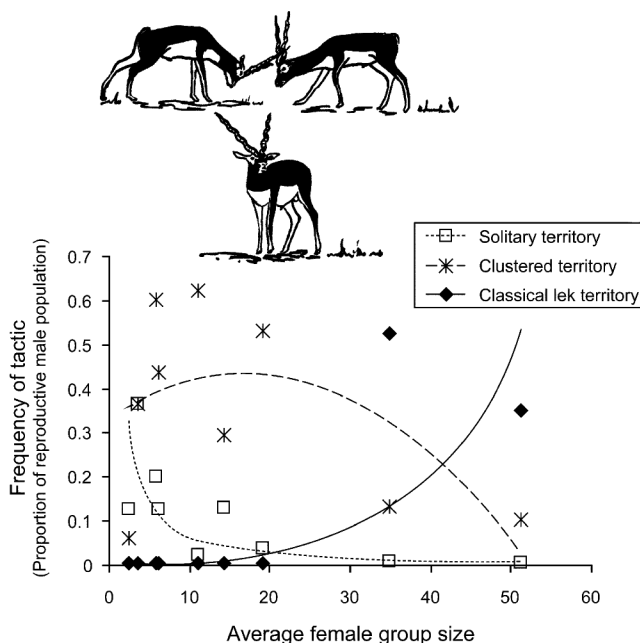


Figure 2. Relative frequencies of male mating tactics in relation to local female numbers (represented by female group size) across nine blackbuck populations (1998–1999). The main male mating tactics in blackbuck are (i) to defend solitary, often resource-based territories; (ii) to defend a territory in a cluster (these territories vary widely in size and resource abundance and in the degree to which they are clustered^{23,29}); and (iii) to defend a territory on classical leks (aggregations of many, small territories with no resources which are visited by females solely for mating). All tactics are not seen in all populations. Populations vary in the types and frequencies of mating tactics adopted by males. Across populations, an increase in female group size is associated with an increase in costlier tactics. The frequency of males holding solitary territories (low-cost tactic) is highest in populations where females are distributed in small groups and decreases with female group size. The frequency of defending a territory in a cluster (intermediate-cost tactic) increases with female group size, peaks at intermediate group sizes, and declines when females are distributed in the landscape in large concentrations. In populations with the largest female group sizes, classical lekking, the costliest tactic, appears and is predominant; lower levels of all other tactics (and additional sneaking and harassing tactics by juvenile males) are seen in lekking populations. Another male tactic commonly seen in blackbuck is to display to and attempt to mount females in mixed-sex herds. The frequency of this tactic is not shown here because males adopting this tactic have never been observed to mate successfully^{15,16,23}.

Current evidence for frequency-dependent selection in ungulates is inconclusive. This form of selection predicts that in stable populations, alternative phenotypes will have equal fitnesses. This prediction is not supported in ungulates such as Uganda kob and topi, where males who defend lek territories have higher mating success than males who defend solitary territories^{27,40}. However, comparing fitnesses is problematic because populations usually experience some stochasticity and populations may never be at an evolutionarily stable state. Additionally, information on fitness over the lifetime of individuals is essential, but these are difficult to obtain in such long-lived species. Furthermore, fitnesses of alternative phenotypes are only expected to be equal if they are maintained solely by negative frequency-dependence either as alternative genetic strategies or as alternative tactics within a stochastic mixed strategy (see ref. 33). Both these patterns are thought to be rare in wild populations³³. Instead, recent studies suggest that frequency-dependent selection is unlikely to be the only factor maintaining variation and is much more likely to act along with some form of condition-dependence^{4,5,33} and/or with density-dependence⁴⁹. For example, even though age and dominance may influence whether a male bighorn sheep attempts to defend females or to force matings on females, frequency-dependence may influence the switchpoint (age, dominance) at which males switch between the two tactics⁴¹.

Although this paper has focused on alternative tactics, it is important to note that in some ungulates, the tactics are not entirely discrete. In some cases, the variation in mating behaviour is so great that it is difficult to distinguish between tactics (e.g., some populations of fallow deer¹⁰, and blackbuck²⁹). For example, the size and clustering of territories may vary so much that it is difficult to distinguish between resource-based territories, clustered mating territories, and classical lek territories. Although this variation may make categorizing behaviour difficult, such variation provides the opportunity to quantify the shape of the relationship between mating behaviour and potential selective factors. This can give additional insights into the nature of evolutionary processes acting on mating behaviour. Nevertheless, most of the variation that makes certain forms of ungulate male mating behaviour (particularly territoriality) appear to be continuous rather than discrete is seen only when behaviour from multiple populations of a species is pooled together. Within a population, variation in male mating behaviour is more limited and can usually be treated as discrete (e.g., refs 6, 9).

Alternative mating tactics in ungulates: Conclusions and future directions

Discontinuous variation in mating behaviour appears to be widespread among ungulates, especially in bovids and

cervids. Although systematic and detailed studies of alternative mating tactics within ungulate populations are not numerous, some general patterns can be identified.

Males rarely show irreversible patterns, that is, they do not adopt just one tactic throughout their lifetime. Males commonly switch between two or more tactics, often within a single breeding season. For example, in a single season, males in Uganda kob may switch between lek and solitary territories⁴⁰, in fallow deer between lek territories, solitary territories and mixed-sex groups⁵⁰, and in bighorn sheep between female-defence and harassing tactics⁴¹.

Alternative mating tactics within a population are most likely maintained as part of a conditional strategy influenced by multiple internal and external factors. Tactics that males adopt commonly change with age, size and condition. Young males are more likely to adopt sneaking or harassing tactics and pursue and try to mate, sometimes forcibly, with oestrous females, whereas adults may adopt other tactics such as harem-defence, resource territories or lek territories^{6,11,41}. Relatively large males may adopt high-cost, high-benefit tactics such as lekking, while smaller males may be forced to adopt tactics that yield fewer mating benefits^{27,40}. Similarly, males may switch between tactics in response to changes in condition. Other than these internal factors, female and male local densities appear to be important external factors contributing to the maintenance of alternative mating tactics within a population. There is also some evidence that oestrus synchrony is important. The mechanisms by which these external factors influence the costs and benefits of alternative mating tactics are still not understood.

Much work remains to be done on the factors maintaining alternative male mating tactics, and more generally, intraspecific variation in ungulates. First, to understand the costs and benefits of alternative phenotypes and the factors influencing them, data collected over an individual's lifetime (or a significant portion of it) are needed. Such data are still limited to a few species (e.g., red deer, bighorn sheep). Second, most studies have focused on evolutionary questions and less is known about proximate mechanisms underlying alternative mating tactics, such as the information that individuals use in the decision-making process, the factors that affect the condition of individuals, and the influence of factors acting early in the development of individuals. Third, the role of frequency dependence in maintaining alternative mating tactics in ungulates is still not well known. Frequency-dependent selection will most likely influence the point at which an individual switches from one tactic to another. For example, in lekking species, it is likely that the mating success of a male within a lek decreases as the number of males joining a lek increases (as is reported in some lekking birds⁵¹). When this happens, males who switch from lekking to other tactics such as resource territories may do better. Finally, most work on mating behaviour in ungulates has focused on male behaviour. Much less is known about female behaviour and

how it affects male mating tactics; the factors that influence female mating behaviour; and whether females show alternative mating tactics. Behavioural variation in ungulate populations is an exciting area of research, which is likely to provide insights not only into the evolution of ungulate behaviour but also, more generally, into the evolution of individual decision-making.

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