The Lekking Puzzle*

The Evolution of Costly Mating Behaviour

Kavita Isvaran

Males display diverse behaviours to try to obtain mates. Some male mating tactics, such as lekking, are spectacular because of the behaviours that they involve. Lekking males establish tiny, clustered territories without any resources attractive to females. They perform eye-catching displays, hardly feed, and compete intensely. Here, I describe the challenge that lekking poses to our understanding of the evolution of male mating behaviour. I outline the main hypotheses proposed to explain this behaviour and synthesize the evidence for these hypotheses from empirical tests in wild populations.

Kavita Isvaran is an Associate Professor at the Centre for Ecological Sciences at IISc, Bangalore. She is a behavioural ecologist who focuses on animal behaviour and life histories, particularly social and reproductive traits. She is also interested in the consequences of evolved behavioural and life history traits for populations.

Imagine a hundred male antelope confined to a small arena in a large grassland. There are no visible walls or fences, but each male moves only within a tiny space that has no food or water. A few males stand or lie down but most march around stiffly, with their heads and horns bobbing, their ears held down, and their tails curled up. Frequent fights break out at the boundaries of their tiny spaces. Some of these fights end soon but others are intense. Males lock horns, wrestle, and attempt to gore their opponent. What are these males doing? Why are they not ranging widely in the grassland, feeding and resting like the other antelope in the landscape? This extraordinary behavioural phenomenon, called lekking, is extremely rare in the animal world. A small set of insects, fish, frogs, lizards, birds and mammals are known to show this behaviour [1]. Lekking males do what they do, not for food or shelter or safety from predators but for mates (*Figure* 1).

Keywords
Mating behaviour, lekking, mate choice, male-male competition, sexual selection.

Animals spend much of their life in a quest for mates. The ways in which animals try to get mates can be surprisingly diverse.

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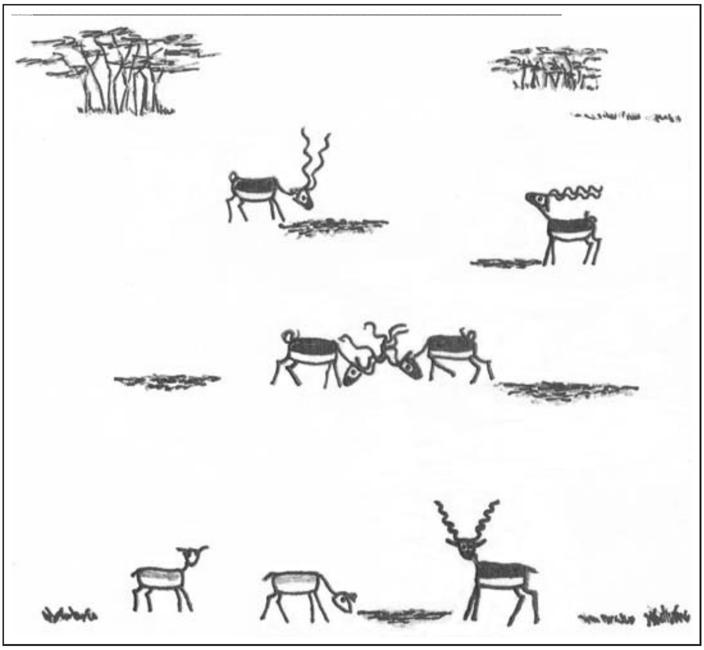

Figure 1. A cartoon depicting a part of a blackbuck lek. Blackbuck, *Antilope cervicapra*, are antelope native to the Indian subcontinent. They are found in dry grassland and scrub habitats, feeding on grass, and living in groups. Males are larger than females, with a black/dark brown and white coat and long spiralling horns. Females are hornless and light brown and white. In lekking blackbuck populations, at the peak of the mating season, the main lek may have as many as 100–150 males clustered together. Each male defends a tiny territory within the lek, creates large scent marks with urine and dung, and displays to females who visit the lek only to find mates.

These mating tactics, that is, the behaviour that individuals show to get mates, can differ from species to species, from population to population, or even from individual to individual within a population (*Box* 1). In many animals, males put in more effort to get mates than do females. This seems to be related to the effort that females and males invest in producing young and caring for them. In many species, female reproductive success, that is, the number of offspring they can produce over their life time, is limited by the quantity of resources they can obtain. In contrast, male reproductive success is limited by how many females a male can successfully mate with. So, males are expected to compete with other males and try to mate with as many females as possible. On the other hand, females are expected to be choosy and only mate with one or a few males competing for them [2, 3]. As a result of the strong competition for mates, males have evolved different behavioural tactics to win in this competition and successfully obtain mates. These tactics are designed to increase the chances of encountering females, attract them so that they choose to mate with the focal male, and keep away other males from po-

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Box 1. Glossary of Terms

Mating Tactic: A specific set of behaviours that together form a means to acquire mates (e.g., female-defence, resource-defence, lekking)

Mating Strategy: An evolved heritable rule that specifies the tactic (or tactics) to adopt. Mating strategies can be of different types. A strategy might specify that an individual adopts only a single tactic throughout its life. Or a strategy could specify that an individual adopts different tactics during its life. Some examples of strategies that specify multiple tactics are conditional strategies where individuals adopt different tactics under different external or internal conditions (e.g., lekking if large in size and resource-defence if small in size), and stochastic mixed strategies where individuals adopt different tactics with certain probabilities that have been selected for.

Mating system: The outcome at the population level of the mating behaviour shown by males and females.

Lek: A territorial aggregation in which each male holds a small territory without conventional resources, like food and water. The main function of this territory is to provide a space in which the resident male perform displays to try to attract females to mate with him. The aggregation is called a lek. Females visit the lek only to mate and not to find food or water or any other resource.

Sexual Selection: An evolutionary process that involves competition between individuals of the same sex and same species for mates. The types of traits that evolve through this form of selection are mainly traits that provide an advantage either in direct competition between individuals for access to mates or in indirect competition where individuals of the same sex compete to be chosen by potential mates.

tential mates. Because obtaining mates is a key component of evolutionary fitness, understanding the evolution of mating tactics has been an important focus in the fields of animal behaviour and evolution.

Mating Tactics

To understand the evolution of male mating tactics, studies have successfully used an economic approach. The idea is that males in a population have a set of mating tactics that they could potentially adopt. Each tactic has associated costs and benefits. For example, a tactic may be energetically costly or may make the male very conspicuous to predators. The main benefit is the number of mates a male is able to get. To be more precise, since females mate with multiple males in many species, the benefit is better

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measured as the number of fertilisations the male gets. The tactic that maximises net benefit (i.e., benefit-cost) should be favoured because it results in the greatest fitness. This tactic is often called the 'optimal tactic' and is expected to be adopted by males in the population. The optimal tactic can dramatically differ from one ecological context to another, because ecological conditions can strongly affect costs and benefits. For example, consider a mating tactic that attracts many females but is very conspicuous. In an area with high predator densities, such a tactic may perform badly when compared with less conspicuous tactics that attract fewer females and also fewer predators. However, if predator densities are low, the conspicuous tactic may be most successful because the benefits of attracting females now outweigh the costs of being attacked by predators. Studies have demonstrated how variation in ecological conditions among populations can result in the evolution of different male mating tactics in the different populations. Like ecological conditions, several other factors can affect the costs and benefits of mating tactics; some prominent examples of such factors are population density, sex ratio, length of mating season and the distribution of breeding females in space and time [2]. Together with a cost-benefit approach, a game-theoretic approach has also been used to figure out why one or more mating tactics are seen in a population. The costs and benefits that a male experiences from displaying a particular mating tactic may be affected not only by conditions like predators, food, and the number of females available but also by what other males in the population are doing. For example, if many males adopt a tactic of aggressively defending as many females as possible, an alternative mating tactic of covertly attempting to mate with females, without attracting the attention of the dominant males, may yield higher benefits.

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These different approaches have provided us with a good understanding of some male mating tactics. For example, in some mammals, females move in groups. Males join these groups, either only during the mating season or for longer periods. The resident males then defend these groups from other males, who either overtly attempt to take over the groups or covertly attract the females to mate with them outside these groups. This male mating tactic is called 'female-defence'. In some mammals, males do not try to directly defend females. Instead, they establish territories in areas with resources that females find attractive, like food and water. When females visit these territories for resources, the male owner of the territory performs displays and courts the females. The owner also tries to keep out other males from his territory. This male mating tactic is called 'resource-defence'. We think we understand the ecological conditions that select for female-defence versus resourc–defence. When females move alone or in small groups, males, either alone or with other males, can successfully defend female groups. However, when females move in very large groups and/or over large areas, female-defence may not be economical. Instead, males may gain higher net mating benefits if they maximise encounter rates with females by defending resources that attract females. Like female- and resource-defence, there are several other male mating tactics, whose evolution is quite well-understood [2, 3].

Lekking

Lekking stands out as a male mating tactic whose evolution is still not fully understood. Many different hypotheses have been proposed to explain the evolution of this male mating tactic [1]. To recap the puzzle, lekking males defend tiny territories that are clustered and that do not contain resources like food and water. Females visit these territorial aggregations, called leks, apparently only to mate, and usually leave soon after mating. Lekking appears to be very costly compared with other male mating tactics like female-defence and resource-defence. Lekking males hardly leave their territories to feed, perform energetically costly displays, and fight frequently [4]. The key question that hypotheses for lekking focus on is, why do males cluster their territories so closely in a tiny part of the available habitat and consequently, compete intensely, rather than establish large territories away from each other that would provide food and also minimise

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contact (and associated costs of aggression) with other males?

Some Popular Hypotheses

Let us examine some of the most popular hypotheses for the evolution of lekking [1]. Some researchers have called lekking a 'default' male mating tactic that performs better than other tactics under certain ecological conditions [6]. Specifically, when females move in very large groups and their movement patterns are erratic and unpredictable, it may not be economical for males to either try to defend groups of females from other males because the groups are too large to defend successfully or to defend resource territories because females may not predictably visit these areas. Under such conditions, lekking may act as the default mating tactic. This hypothesis still does not explain why we should see lekking and not some other default mating behaviour.

The 'hotspot hypothesis' proposes that when females have large home ranges, males are most successful when they defend territories in the intersection of many female home ranges. Thus, leks form not because males actively try to cluster their territories but because all these males select the same hotspots where encounters with females are maximised.

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Evidence and Importance

What is the evidence from wild populations for these different hypotheses? Hypotheses of lekking have been tested in a wide variety of species, including insects, fish, reptiles, birds, and mammals. Reviewing this literature, we can make several broad conclusions. First, the process that favours the evolution of lekking seems to differ from species to species. For example, studies of a lekking fish and a lekking antelope find the strongest evidence for the female-choice hypothesis [5, 6], whereas a study of the marine iguana finds evidence for the hotshot hypothesis [7]. This suggests that there may not be a general process underlying the evolution of lekking [5]. Second, several studies report that multiple processes may act within the same population to favour lekking. For example, at a large spatial scale, territorial males may gather in areas of high female densities (hotspot hypothesis) (*Box* 2, *Figure* 2). Further clustering of these territories could result from a female preference for mating with clustered males (female-choice hypothesis). Third, perhaps the most striking conclusion is that in many populations, despite detailed studies, the processes favouring the evolution of lekking are still not clear. These studies, which have mostly relied on natural variation in behaviour, highlight the need for innovative approaches, including field experiments, to distinguish between the different hypotheses. Lekking, thus, continues to pose a challenge to our understanding of the evolution of mating behaviour.

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Box 2. Lekking in Blackbuck

I began studying lekking in the antelope, blackbuck *Antilope cervicapra*, 25 years ago, for my Masters and then PhD research. Intrigued by its variable, and sometimes extraordinary, social and mating behaviour, our research group in IISc continues to study different populations of blackbuck [e.g., 4, 5, 8, 9]. This antelope is one of the very few animal species known to lek. Only two populations of blackbuck are reported to lek. In all the other populations, males adopt resource-defence and female-defence mating tactics to try to get mates. The variable mating system of blackbuck provides an excellent opportunity to study how changing ecological conditions may favour different male mating tactics. By studying many different populations, we were able to show that lekking in blackbuck occurs only when local densities of females are high. This is probably because female numbers act as a ceiling on mating benefits. Only when female numbers are high do lekking males gain sufficient mating benefits to outweigh the high costs of this mating tactic. Under low female densities, males adopt low-cost mating tactics, like defending solitary dispersed territories (*Figure* 2). Male mating tactics vary even within a blackbuck population. The across-population and within-population variation also allow us to test hypotheses for the evolution of lekking. In blackbuck, it is clear that lekking is an evolutionary outcome of multiple processes. At large spatial scales, the hotspot hypothesis explains the formation of leks, but at smaller spatial scales, other processes like female-choice seem to be important. The level of variation seen in blackbuck is quite intriguing because even individual males can vary in their display, courting and fighting behaviour. We study the individual-level variation in behaviour to understand how changing costs and benefits shape behaviour.

Together with providing the opportunity for testing our general understanding of how mating tactics evolve, lekking is ideally suited for a wide range of questions on mating behaviour. First, males in lekking populations appear to compete very strongly for mates. In almost all lekking populations, only a few males gain most of the matings, and most males do not mate at all. This sets the stage for strong sexual selection, which is the evolutionary process that favours male traits that provide an advantage in the competition for mates. This advantage could be in the form of traits that help males either win in fights (male-male competition) or win in the competition to be chosen by females (mate choice). So, it is not surprising that lekking males show extreme aggression, and exaggerated conspicuous traits, like bright ornaments and striking visual displays. As a result, lekking systems have been the focus of studies that explore how male phenotype is shaped by strong male-male competition and female mate choice.

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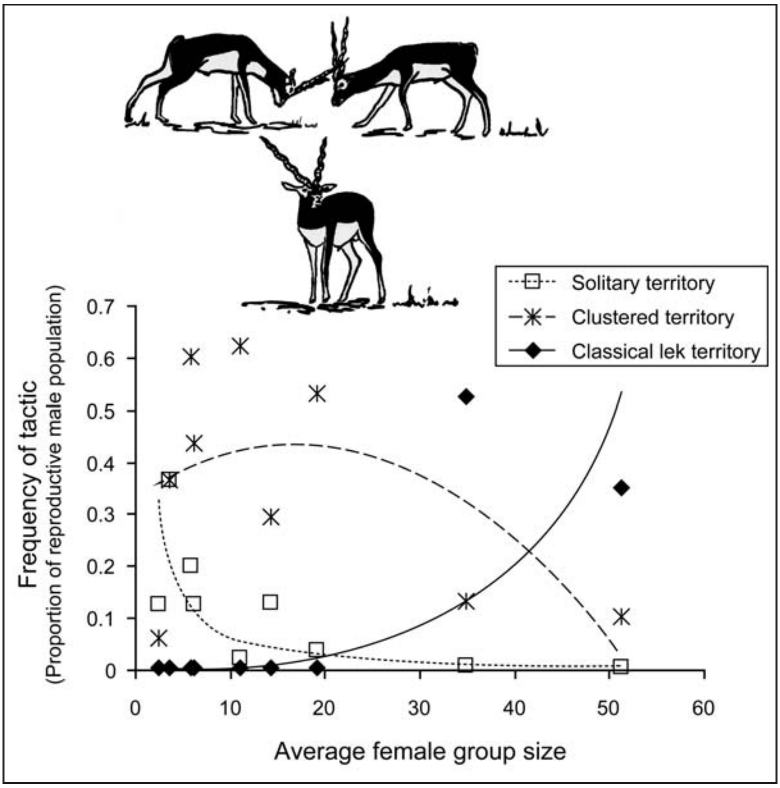

Figure 2. Male mating tactics vary widely both across different populations of blackbuck and within a population. Data on the relative frequencies of three different tactics in each of the nine different blackbuck populations are shown here. Local female numbers (indexed well by female group size) seem to affect the relative frequency of different male mating tactics in a blackbuck population. The costly lekking tactic dominates in populations with high female numbers and disappears when female numbers are low. The low-cost tactic of defending a solitary resource-based territory is most common under low female numbers, while the moderately costly tactic of defending a clustered territory with some resources is most common under intermediate female numbers. (Figure reproduced with permission from K Isvaran, Variation in male mating behaviour within ungulate populations: patterns and processes, *Current Science*, Vol.89, pp.1192–1199, 2005.)

Second, lekking systems are also unusual in that females appear to be in a position to move freely between males and choose one or more mates. So, many studies have focussed on the dynamics of female choice, that is, how females sample males, what information females use to choose mates, and what females gain by being choosy. Third, historically, studies of mating behaviour focused on males competing with each other for females and females choosing between different males. However, evidence is accumulating to show that mating behaviour is much more diverse. For example, both males and females may compete intensely and be choosy on leks of the topi, an African antelope [6]. An exciting line of research is to establish a predictive framework for the levels of competition and choice that males and females should show. In addition, recent work has uncovered other fascinating research questions on leks, including how kin selection, cooperation between males, and social networks may affect the formation of leks and mating dynamics on leks. Overall, the rare and extraordinary lekking system is likely to continue to provide insights into the evolution of complex male and female social behaviour.

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Address for Correspondence
Kavita Isvaran
Centre for Ecological Sciences
Indian Institute of Science
Bengaluru 560 012, India.
Email: kavita@iisc.ac.in