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7-10-2008

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Recommended Citation

Van Horn, R., Watts, H. & Holekamp, K. Do female hyaenas choose mates based on tenure?. *Nature* 454, E1 (2008). DOI: 10.1038/nature07122

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Do female hyaenas choose mates based on tenure?

Arising from: O. P. Höner *et al.* *Nature* 448, 798–801 (2007)

In their investigation into whether female mate-choice drives male dispersal, Höner *et al.*¹ argue that female spotted hyaenas (*Crocuta crocuta*) prefer mates whose tenure in the social group is less than the females' age, to avoid paternal incest, and suggest that male dispersal reflects this preference. However, we are not persuaded that females choose mates on the basis of tenure because Höner *et al.*¹ overlook the alternative hypothesis that dispersal status itself is important in female mate-choice^{2,3}, such that females prefer immigrants over natal males. Like mate-choice based on tenure, choice based on dispersal status reduces the risk of incest.

Female hyaenas discriminate immigrants from natal males⁴, so if natal males sire offspring in proportion to their abundance, this argues against female choice based on dispersal status. Behaviourally, 11% of Ngorongoro Crater males "started their reproductive career" in their natal groups¹. On the basis of comparable behaviours, 68% of males born in a Masai Mara population also did so⁵. (Note that this *Crocuta* population is the same one from which we derived the data for our Fig. 1.) Nevertheless, adult natal males were less likely to father any cubs than were immigrants² and natal males sired only 2.7% of cubs, although they comprised more than 20% of adult males² ($\chi^2 = 16.04$, degrees of freedom, d.f. = 1, $P < 0.001$). Thus, prior paternity data² indicate that females avoid mating with natal males, preferring immigrants.

Mate-choice in hyaenas often seems, perhaps coincidentally, to reflect both choice based on tenure and choice based on dispersal status. Of 76 litters born in the Masai Mara study population (see above), 51 (67.1%) were sired by males consistent with both choice based on tenure and dispersal status (Fig. 1). Therefore, we focus on the remaining 25 litters, which allow us to distinguish between the two competing hypotheses. Of these 25 litters, 22 (88%) were sired by immigrants present in the clan when the mothers were born, supporting choice based on dispersal status, but conflicting with choice based on tenure. However, only 3 out of 25 litters (12%) were sired by natal males born after the mothers, supporting tenure-based choice while conflicting with choice based on dispersal status. Thus, most of our informative litters support female choice based on dispersal status, and conflict with choice based on tenure. Although most (89.6%)

Ngorongoro Crater litters seem to support tenure-based mate-choice¹, Höner *et al.*¹ present no paternity data comparing reproductive success between immigrants and natal males. Without such data, we cannot know whether Ngorongoro Crater females prefer immigrants as mates.

Furthermore, Fig. 1 and related analyses of Höner *et al.*¹ may derive from female preference for immigrants², coupled with age differences between natal females and immigrant males. If litters in Fig. 1 of Höner *et al.*¹ were sired primarily by immigrants, as indicated by our data, and Ngorongoro Crater males immigrate when about 4 years old, as elsewhere^{6,7}, then their Fig. 1 and ours both compare females of age X years with males aged $(X + 4)$ years. Males survive no longer than females⁸, so both figures may reflect a dearth of old males, not tenure-based mate-choice.

We do not suggest that females in this or other species choose mates based solely on male dispersal status. However, male-biased dispersal is common among mammals^{9,10}, so dispersal-based mate-choice could occur in many species. By contrast, tenure-based choice is possible only in social systems like that of *Crocuta*, so it cannot explain widespread sex differences in dispersal behaviour. In addition, because spotted hyaenas discriminate maternal kin, paternal kin, and sires from non-kin^{11,12}, females might choose mates based on several criteria. However, the role of male tenure in female mate-choice¹ remains unclear.

METHODS

We quantified female mate-choice in a large Kenyan social group by classifying hyaenas as adults at 24 months of age¹, considering immigrants as residents 3 months after their arrival¹, and assigning kinship by paternity analysis². We assigned paternity to 76 out of 110 litters born in 1989–2000. Five litters were sired by multiple males. Such litters occur near Ngorongoro Crater⁶, but it is unclear how Höner *et al.*¹ treated such litters; for these, we plot the sires' average tenure.

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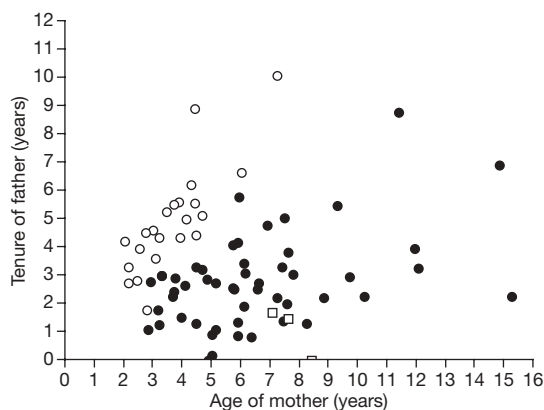


Figure 1 | The relationship between age of the mother on the date of conception, the tenure of the sire, and the sire's dispersal status. ($N = 76$ litters.) Filled circles, litters sired by immigrants who joined the clan after the mother was born, supporting mate-choice based on both dispersal status and tenure. Open circles, litters sired by immigrants who were present in the clan when the mother was born, supporting choice based on dispersal status but not tenure. Open squares, litters with a natal male sire younger than the mother, supporting choice based on tenure but not dispersal status.

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doi:10.1038/nature07122

Höner et al. reply

Replying to: R. C. Van Horn, H. E. Watts & K. E. Holekamp *Nature* 454, doi:10.1038/nature07122 (2008)

We demonstrated that female mate-choice, rather than male inbreeding avoidance, resources or male–male competition, drives male-biased dispersal in spotted hyaenas (*Crocuta crocuta*)¹. We further showed that females use two simple rules based on male tenure to choose their sires, and that males gain substantial fitness benefits by responding to these preferences¹. Van Horn *et al.*² accept our principal conclusions but claim that females base mate-choice on dispersal status rather than tenure. Their argument overlooks the fact that at least one of the two female mate-choice rules cannot be explained by dispersal status, and it is based on statistical analyses and a selection of males that we consider inappropriate for tests of female mate preference.

Young female spotted hyaenas prefer to breed with short-tenured rather than long-tenured males^{1,3}. This preference cannot be explained by a rule based on dispersal status but must involve tenure-based rules such as those suggested by us¹.

In spotted hyaenas, many natal males do not display sexual interest in females before they disperse^{1–4}. Because females are unlikely to consider such males as potential mates, they should be excluded from tests of female mate preferences^{1,3,5,6}, as is common practice among primatologists^{5,6}. Any appropriate test of female mate preference then considers the number of reproductively active natal males and immigrant males at the conception of each litter and averages the results over all litters per female to yield one data point per female^{1,7}. The comparisons by Van Horn *et al.*² of the percentage success of natal males and immigrant males in the pools of all natal males and all immigrant males present during their study do not recognize these aspects.

First, their tests of preference include natal males without considering their reproductive activity. Their² quote of 68%⁸ of natal males in their *Crocuta* study group (in contrast to 11% in our study population¹) showing reproductive behaviour to females is puzzling given that testosterone concentrations of natal males resemble testosterone concentrations of juvenile non-reproductive males⁹. In the paternity analysis of Van Horn *et al.*² (citing ref. 10), natal males are assumed not to be candidates and therefore presumptively excluded if they are a relative (at $r \geq 0.125$) of the female, thereby reducing the chance of natal males being identified as sires. Thus, the tests of preference by Van Horn *et al.*² and a previous paternity study on the same clan¹⁰ compare the reproductive success of unrelated natal males with a pool comprising reproductively active and inactive, sexually immature, related and unrelated natal males, thereby reducing the percentage of successful natal males and favouring immigrant males^{6,7}.

Second, Van Horn *et al.*² did not take into account the fact that male reproductive success strongly increases with tenure^{3,10}. With their method, reproductive success becomes skewed towards long-tenured immigrant males¹⁰ owing to significant differences in mean

tenure between immigrant males and natal males^{3,10}. This demonstrates the importance of tenure, not dispersal status.

Third, for their 22 litters apparently not conforming to the tenure-based rule, Van Horn *et al.*² do not provide any evidence or test that compares the availability of immigrant males and reproductively active natal males on the dates of conception, nor the availability of males born/immigrated before and after the female's birth.

Van Horn *et al.*² state that our result that females avoid males present when the females are born¹ may reflect a lack of such male candidates. This is incorrect because our test considered the proportion of candidate males that initiated their reproductive career before and after the females were born¹. And if we consider only those litters where females can choose between both males that initiated their tenure before and after the female's birth, they still strongly avoid males present when they were born (Wilcoxon signed-rank test, $n = 54$ females, $P = 0.0001$).

Do females prefer immigrant males in our eight study groups? No: the reproductive success of natal males during their reproductive tenure¹ did not differ from the mean reproductive success of their immediate immigrant male predecessor and successor during the same duration of tenure (Wilcoxon signed-rank test, $n = 12$, exact $P = 0.148$, power = 0.35).

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doi:10.1038/nature07123