

Why do some males choose to breed at home when most other males disperse?

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Dispersal is a key driver of ecological and evolutionary processes. Despite substantial efforts to explain the evolution of dispersal, we still do not fully understand why individuals of the same sex of a species vary in their propensity to disperse. The dominant hypothesis emphasizes movements and assumes that leaving home (dispersal) and staying at home (philopatry) are two alternative strategies providing different fitness. It suggests that only individuals of high phenotypic quality can pursue the most beneficial strategy; the others are left to do a “best-of-a-bad” job. An alternative hypothesis emphasizes settlement decisions and suggests that all individuals pursue a single strategy of choosing the breeding habitat or group with the highest fitness prospects; choosing the natal group (philopatry) and choosing a nonnatal group (dispersal) are then outcomes of these decisions. We tested both hypotheses using a long-term study of a free-ranging population of a group-living carnivore, the spotted hyena. We combined demographic data with data on dispersal-relevant phenotypic traits, breeding-group choice, survival, and reproductive success of 254 males. Our results contradict the best-of-a-bad-job hypothesis: philopatric males and dispersers were of similar phenotypic quality, had similar fitness, and applied similar settlement rules based on the fitness prospects in groups. Our findings demonstrate that the distribution of breeding partners can be more important in shaping dispersal patterns than the costs associated with the dispersal movement. The study provides novel insights into the processes leading to the coexistence of philopatry and dispersal within the same sex of a species.

INTRODUCTION

Dispersal is one of the most important yet least understood drivers of ecological and evolutionary processes (1, 2). In almost all sexually reproducing species, some individuals disperse from the habitat or group in which they were born and attempt to breed elsewhere, whereas others either never disperse or only do so after a period of philopatry. Dispersal patterns in terms of the proportion of dispersing individuals or the distances traveled, however, vary greatly between species, populations, and sexes (3–5). Previous theoretical and empirical studies have advanced our understanding of the evolution of dispersal and the drivers of sex-biased dispersal (2, 5–8). Yet, we currently know little about the evolutionary processes leading to the coexistence of dispersers and philopatric individuals within the same sex of a species (8–10).

The evolutionary theory predicts that individuals should assess the quality of potential breeding habitats and disperse if the fitness prospects in the natal or current habitat are lower than those elsewhere, after accounting for the costs of between-habitat movements (8, 11, 12). Dispersal may generally confer fitness advantages by reducing potential costs of kin competition and inbreeding or by leaving a deteriorating habitat, whereas philopatry may confer advantages through familiarity with the natal territory and conspecifics, as well as kin cooperation (2, 4, 7). The dominant hypothesis to explain the coexistence of philopatry and dispersal suggests that, for a given sex of a species, one strategy provides higher fitness than the other but that only individuals of high phenotypic quality can pursue this strategy and maximize their fitness (4, 10, 13). In line with this hypothesis, the high proportion of male dispersal observed in many group-living mammals (3) was suggested to reflect a selective advantage of dispersal (4). Because gathering information about breeding

groups [“prospecting” (14)] and settling in a group are usually considered costly (8, 15), only males of high searching efficiency, high competitive ability, or high social skills were suggested to succeed in settling and securing a breeding position in a new group (10, 13, 16, 17). As a result, male philopatry in group-living species with a high proportion of dispersers has been either neglected or considered as a “best-of-a-bad” job pursued by phenotypically inferior males (4).

This hypothesis emerged from studies that focused on the costs and benefits of the movement associated with dispersal (4, 8, 18). It assumes that moving away from or staying in the natal environment is a trait that falls under natural selection and that philopatric individuals and dispersers experience different selection pressures and breed in environments of different quality. Although these assumptions may be valid for some species, the costs and benefits of the dispersal movement may only play a minor role in shaping dispersal patterns in many others (19). For example, in species with large social groups and moderate reproductive skew within sexes, the genetic structure of the population may be weak, and leaving the natal group may not necessarily reduce the potential costs of kin competition and inbreeding (20–22). Males may also prospect and disperse at low search and survival costs if gathering information does not necessitate emigration from the natal group and dispersal distances are short (23, 24). In such systems, males that eventually become philopatric may also prospect, follow the same process of breeding-group selection, apply similar settlement rules, and have the same fitness prospects as dispersers. This has rarely been considered by theoretical studies within the dispersal context (19).

To our knowledge, no study has previously investigated whether the coexistence of philopatric males and dispersers (i) results from high dispersal costs preventing phenotypically inferior males from dispersing or (ii) is a consequence of all males applying the same rules of breeding-group choice and choosing philopatry or dispersal depending on whether the natal group or a nonnatal group offers the highest

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fitness prospects. We tested predictions derived from these two hypotheses on a free-ranging population of a group-living mammal, the spotted hyena (*Crocuta crocuta*), for which we previously identified female mate choice as the main driver of male-biased dispersal (25). We combined long-term demographic data from the entire population of the Ngorongoro Crater in Tanzania, comprising eight social groups (“clans”), with data on breeding-group choice, dispersal-relevant phenotypic traits, survival, and reproductive success for 41 philopatric males and 213 dispersers. This comprehensive approach provided the rare opportunity to assess the causes and fitness consequences of male philopatry and dispersal in a social mammal in a population still subjected to the processes of natural and sexual selection.

First, we tested whether philopatric males and dispersers differed in their phenotypic quality before clan choice. In spotted hyenas, males are not evicted from their natal clan by other clan members (26). Before choosing a clan for breeding, both philopatric males and dispersers undertake excursions to other clan territories and may thereby assess their fitness prospects in potential destination clans (25). During these excursions, males may experience aggression from resident males (27). A male’s prospecting behavior, his chances to settle in a new clan, and the period of time required until clan choice may therefore be influenced by his searching efficiency, his ability to overcome social challenges, and whether he grew up in the chosen clan (16, 28). Because, in spotted hyenas, sons of high-ranking females grow faster, start reproducing earlier, and are more likely to disperse to clans offering higher fitness prospects than lower-born males (29), they may be of higher phenotypic quality with respect to clan choice (16). Thus, if prospectation and settlement incur high costs and these costs prevent phenotypically inferior males from dispersing, philopatric males should comprise a higher proportion of low-born males.

Second, we tested whether philopatric males and dispersers differed in their fitness in terms of the number and quality of offspring sired, age at first reproduction, and survival. Spotted hyenas live in multimale, multifemale social groups, structured by strict linear dominance hierarchies, in which females and their offspring are dominant over immigrant males (30, 31). A male’s chance to be chosen as a sire mainly depends on his investment in developing friendly relationships with females rather than his body size or fighting ability (32, 33). Reproduction within a clan is not monopolized by high-ranking individuals, and females and males breed promiscuously (33). Male social rank may nonetheless influence male reproductive success because high-ranking males have privileged access to food and females, and may afford to spend more time and energy consorting and developing relationships with females compared to lower-ranking males. Dispersal and philopatry have different implications for the social rank of males in hyenas; dispersers join the new clan at the bottom of the male social hierarchy and only increase in rank with increasing tenure in the clan, whereas philopatric males dominate all immigrant males (30, 34, and this study). Male reproductive success may be additionally influenced by male origin because males that grew up in the chosen breeding clan (“native males”) are more familiar with the females and have better knowledge about their quality and preferred whereabouts than males that grew up in another clan (“foreigners”). If male social rank and origin do influence male reproductive success, philopatric males should sire their first offspring earlier and sire more offspring than dispersers. Similar to top-ranking, long-tenured dispersers (30), philopatric males may mainly invest in consorting high-ranking females and sire more offspring of high reproductive value (35) compared to dispersers.

Higher social rank and the associated preferential access to food within the clan territory may additionally cause philopatric males to be in better physical condition and survive better than dispersers.

Third, we investigated whether philopatric males and dispersers differed in the rules they apply when choosing their breeding clan. Female hyenas have complete control over mating (36) and apply mate-choice rules to avoid incest; they prefer sires that were born into or immigrated into their clan after they were born (25), and females older than 5 years additionally prefer males with long tenures (33). The number of females that comply with these rules on the date a male chooses a clan defines the pool of females most likely to breed with a male, that is, clan quality. Previously, males were shown to prefer high-quality clans (25). In our system with fluctuating numbers of females in clans, a male’s natal clan may occasionally contain the highest number of likely breeding partners. We therefore tested whether, as predicted by habitat selection models, the quality of male clan choice and the propensity to choose philopatry resulted from the combination of (i) male preference for high-quality clans, (ii) the relative availability of high-quality clans among natal clans, and (iii) the predicted benefits associated with philopatry.

RESULTS

Phenotypic quality of males and age at clan choice

The proportion of philopatric sons of low-ranking (0.21, $n = 8$), medium-ranking (0.44, $n = 17$), and high-ranking (0.36, $n = 14$) females did not differ from the proportion of dispersers that were sons of low-ranking (0.19, $n = 36$), medium-ranking (0.30, $n = 59$), and high-ranking (0.51, $n = 99$) females [Pearson’s χ^2 test; $\chi^2 = 4.2$, degree of freedom (df) = 2, $P = 0.12$]. The age at which philopatric males chose their first breeding clan (3.3 ± 0.9 years, $n = 40$ males with known birth date) was similar to that of dispersers (3.5 ± 0.7 years, $n = 177$; $U = 3130.5$, $P = 0.25$). The age at clan choice was not influenced by male origin [ordinary least-squares linear model (LM), likelihood ratio (LR) = 0.07, df = 1, $P = 0.79$] or by maternal social rank (LR = 2.48, df = 1, $P = 0.12$) when we controlled for the identities of the natal clan (LR = 17.75, df = 7, $P = 0.013$) and the chosen clan (LR = 11.86, df = 7, $P = 0.11$; whole model, LR = 1.43, df = 16, $P = 0.009$, $n = 214$ males with known birth date and maternal social rank; see table S1).

Male social rank

Dispersers started their reproductive career in the new clan at the bottom of the male social hierarchy and increased in rank with increasing tenure (Fig. 1). In contrast, philopatric males occupied a high social rank in the male hierarchy from the date of (primary) clan choice until they dispersed (secondary clan choice) or died (Fig. 1).

Tenure and age at first reproduction

Philopatric males sired their first offspring after a shorter tenure (1.1 ± 1.3 years, $n = 25$) than dispersers (1.9 ± 1.5 years, $n = 128$; $U = 994.5$, $P = 0.003$). Philopatric males also sired their first offspring at a younger age (4.2 ± 1.4 years, $n = 24$ males with known birth date) than dispersers (5.3 ± 1.6 years, $n = 100$; $U = 643$, $P < 0.001$). Tenure at first reproduction was significantly shorter for males that grew up in the chosen clan than males that grew up in a different clan (LM, LR = 10.41, df = 1, $P = 0.001$) when controlling for maternal social rank

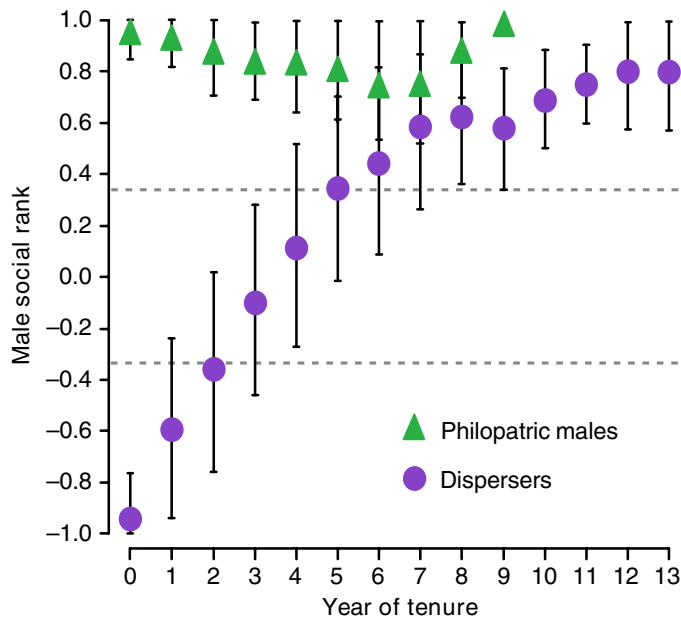


Fig. 1. Change in social rank of philopatric males and dispersers with time spent in the clan (tenure). Data are mean standardized social ranks (symbols) \pm SDs (vertical bars). Standardized ranks were calculated at the start of each year of tenure by distributing ranks evenly between the highest (standardized rank +1) and lowest (standardized rank -1) rank in the hierarchy of sexually active males of a clan. Males with standardized ranks within the top, middle, and lower thirds of the total range (delimited by dashed horizontal lines) were high-ranking, medium-ranking, and low-ranking, respectively.

(LR = 19.47, df = 1, $P < 0.001$), the number of likely female breeding partners at clan choice (LR = 0.59, df = 1, $P = 0.44$), and the identity of the chosen clan (LR = 15.32, df = 7, $P = 0.032$; whole model, LR = 73.33, df = 10, $P < 0.001$, $n = 136$ males with known maternal social rank; see table S2).

Reproductive success

The mean annual reproductive rate of philopatric males with females of all social ranks (0.53 ± 0.43 offspring per year, $n = 28$ males with tenure ≥ 1 year) was similar to that of dispersers (0.69 ± 0.73 , $n = 168$; $U = 2209.5$, $P = 0.60$; Fig. 2). Philopatric males tended to sire more offspring per year with high-ranking females (0.43 ± 0.44) than did dispersers (0.30 ± 0.47 ; $U = 2781.5$, $P = 0.098$), and they sired significantly fewer offspring with medium- and low-ranking females (0.10 ± 0.28) than did dispersers (0.39 ± 0.45 ; $U = 1284$, $P < 0.001$). Philopatric males sired 83% and dispersers sired 39% of their offspring with high-ranking females.

Influence of male origin and social rank on reproductive success

The annual reproductive rate of males native to the chosen clan was lower than that of foreigners [generalized linear mixed model (GLMM), combined effect of male origin and interaction between male origin and year of tenure: LR = 18.95, $P = 0.003$] and increased as male social rank increased (LR = 14.29, $P = 0.003$) when controlling for maternal social rank (LR = 3.62, $P = 0.14$) and the number of likely breeding partners at

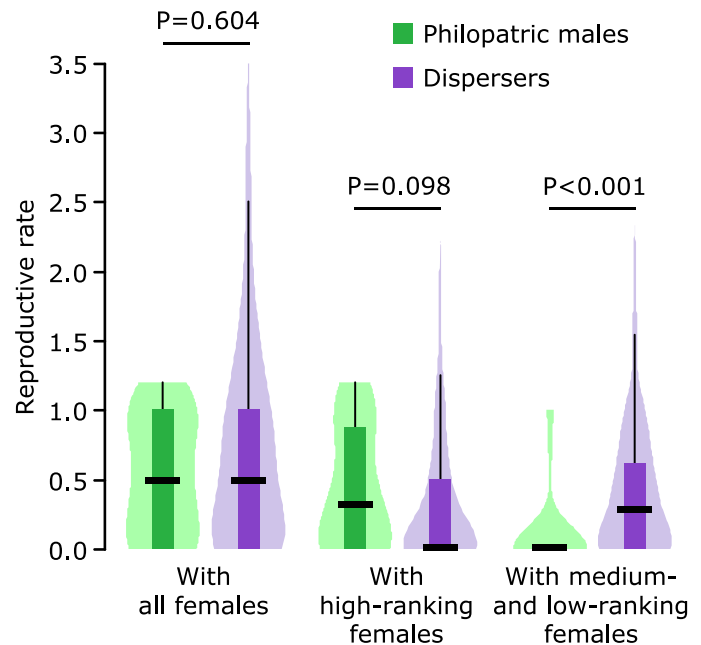


Fig. 2. Comparison of the reproductive rate of philopatric males and dispersers. Reproductive rate is the mean annual number of offspring sired during the first 6 years of tenure. Boxes indicate the interquartile range around the median (horizontal bar), vertical bars represent reproductive rates that lie within 1.5 times the interquartile range, and shaded areas represent the distribution (kernel density estimate) of the data.

clan choice (LR = 0.03, $P = 0.99$; whole model, LR = 71.52, $P = 0.001$, $n = 181$ males with known maternal social rank and tenure ≥ 1 year; see table S3). The annual reproductive rate with high-ranking females was not influenced by male origin (GLMM, combined effect of male origin and interaction with year of tenure: LR = 9.34, $P = 0.16$) and increased as male social rank increased (LR = 15.82, $P < 0.001$) when controlling for maternal social rank (LR = 1.46, $P = 0.41$) and the number of likely breeding partners at clan choice (LR < 0.01, $P = 0.99$; whole model, LR = 56.97, $P < 0.001$, $n = 181$; Fig. 3, A and B; see table S4). The annual reproductive rate with medium- and low-ranking females was lower for native males than foreigners (GLMM, combined effect of male origin and interaction with year of tenure: LR = 39.48, $P < 0.001$) and was not influenced by male social rank (LR = 3.24, $P = 0.12$) when controlling for maternal social rank (LR = 2.99, $P = 0.12$) and the number of likely breeding partners at clan choice (LR = 0.08, $P = 0.89$; whole model, LR = 45.89, $P < 0.001$, $n = 181$; Fig. 3, C and D; see table S5).

Male survival

The survivorship after the date of first clan choice of philopatric males (median from Cox proportional hazards model = 7 years, $n = 41$ males with tenure ≥ 1 year) and dispersers was similar [median = 8 years, $n = 210$; hazard ratio = 1.4, 95% confidence interval (CI) = 0.79 to 2.46, LR = 1.22, df = 1, $P = 0.27$].

Quality of clans and male clan choice

To test whether the quality of natal clans differed from that of non-natal clans and whether this affected male clan choice, we ranked the eight study clans according to the number of likely female breeding

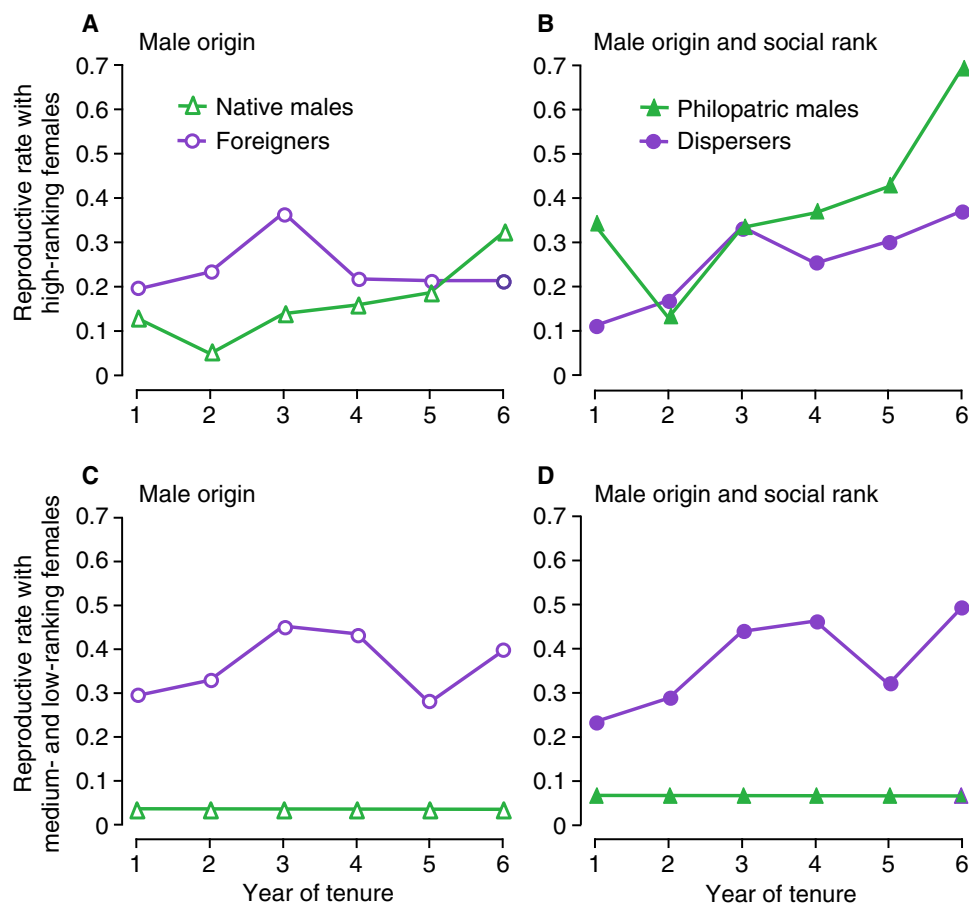


Fig. 3. Influence of male origin and combined effect of male origin and social rank on male reproductive rate. (A to D) Reproductive rate is the mean annual number of offspring sired with high-ranking females (A and B) and medium-ranking and low-ranking females (C and D). Male origin refers to whether males grew up in the chosen breeding clan (native males) or in another clan (foreigners). Data are back-transformed predictions derived from GLMMs that considered the covariates male origin, male social rank, maternal social rank, number of breeding partners at clan choice, year of tenure, and interaction between male origin and year of tenure. Values for the influence of male origin are adjusted means considering all other covariates at their population mean. Values for the combined influence of male origin and social rank are adjusted means computed as for male origin but considering the mean social rank of native males and foreigners, respectively, at each year of tenure. Because male origin and social rank represent the two main traits characterizing philopatric males and dispersers, their combined effect shows the difference in reproductive rate between philopatric males and dispersers.

partners that each clan contained on each date a male chose a clan (25). The distribution of clan qualities of natal clans differed from that of nonnatal clans ($\chi^2 = 152.4$, $df = 7$, $P < 0.001$), with natal clans being less likely to be of the highest quality and more likely to be of the lowest quality compared to nonnatal clans (Fig. 4A). As a result, philopatric males chose clans containing fewer likely female breeding partners (median = 5) compared to dispersers (median = 10; $U = 1621.5$, $P < 0.001$). To test whether philopatric males and dispersers applied different rules of clan choice, we compared the observed number of philopatric males that chose a clan of a given quality with the expected number under the assumptions that (i) philopatric males, similarly to dispersers, base their clan choice on the number of likely breeding partners and (ii) choosing the natal clan does not incur additional benefits or costs as compared to choosing a nonnatal clan. The expected number of (philopatric) males choosing their natal clan when it is of quality i is thereby equal to the product of the proportion of dispersers that chose a clan of quality i (Fig. 4C) and the proportion of

clans of quality i that are natal clans (Fig. 4B, dark gray), multiplied by the total number of males observed to choose a clan ($n = 254$; Fig. 4D). The observed number of philopatric males ($n = 41$, 16.1% of all males that chose a clan) was twice as high as expected in all clan qualities ($n = 19.5$, 7.7%; Wilcoxon signed-rank test, $U = 36$, $P = 0.008$, $n = 8$ clan qualities; Fig. 4D). However, the relative distribution of philopatric males across the eight levels of clan quality did not differ from expectations ($\chi^2 = 0.81$, $df = 7$, $P = 0.99$; Fig. 4E).

Tenure in clan of first choice

Philopatric males were more likely to disperse from their first breeding clan (13 of 26 males with a monitoring period ≥ 6 years) than were dispersers (27 of 146; Fisher's exact test, odds ratio = 2.69, 95% CI = 1.12 to 6.26, $P = 0.021$), and they stayed for a shorter period in their clan of first choice (median from Kaplan-Meier survival analysis = 2.32 years, $n = 41$) than did dispersers (median = 6.03 years, $n = 213$; log-rank test, $\chi^2 = 12.4$, $df = 1$, $P < 0.001$; Fig. 5).

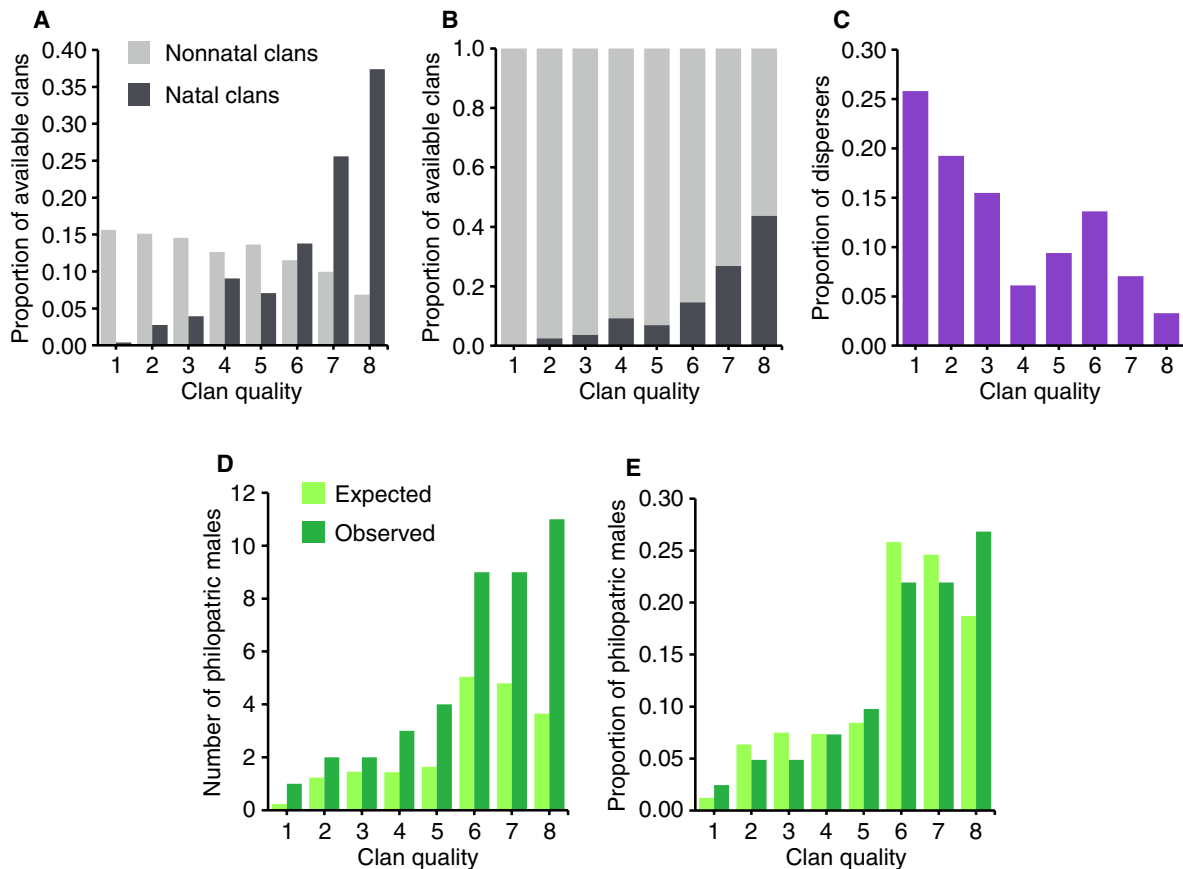


Fig. 4. Effect of clan quality on male clan choice and propensity of philopatry. (A) Distribution of natal and nonnatal clans across eight clan qualities as defined by the number of likely female breeding partners on the date a male chose a clan. Clan quality 1 corresponds to the clan with the highest number of likely breeding partners, and clan quality 8 corresponds to the clan with the lowest number of likely breeding partners. (B) Proportion of natal and nonnatal clans of each clan quality. (C) Distribution of clan choices by dispersers across the eight clan qualities. (D) Expected and observed number of philopatric males that chose each clan quality. (E) Expected and observed proportions of philopatric males across the eight clan qualities.

DISCUSSION

Our findings are inconsistent with the hypothesis that male philopatry is the result of high dispersal costs and a best-of-a-bad strategy pursued by phenotypically inferior males. Philopatric males chose clans containing fewer likely female breeding partners compared to dispersers, but they sired as many offspring as did dispersers and had survival after clan choice similar to dispersers. They also had mothers of similar social rank, suggesting that dispersal propensity was not influenced by the maternal environment during development and that philopatric males and dispersers were of similar phenotypic quality at clan choice. Our finding that philopatric males and dispersers chose a clan at a similar age further indicates that the process leading to philopatry or dispersal required a similar amount of time. The search and survival costs of prospecting and settlement may indeed be low in our population of spotted hyenas and may not differ substantially between philopatric males and dispersers because both undertake short excursions to other clan territories before choosing a clan, dispersal distances are short, and recently settled dispersers frequently return to their natal clan territory and benefit from resuming their natal rank when feeding there (25, 29).

Our results, instead, are consistent with the alternative hypothesis derived from habitat selection theory: The coexistence of philopatric males and dispersers results from all males applying similar rules of clan choice. Philopatric males distributed themselves similarly to dispersers when considering the quality of clans, indicating that they had similar preferences for clans of high quality, that is, clans with the largest number of potential breeding partners. Thus, philopatric males did not choose clans of lower average quality compared to dispersers because they were less choosy, but because natal clans were less likely to be of high quality than were nonnatal clans. The latter is a direct consequence of the rules female hyenas apply when choosing their mates (25); these rules imply that, in nonnatal clans, all females between 1 and 5 years of age on the date of male clan choice are likely to accept the male as a sire, whereas in natal clans, only females older than the male and younger than 5 years are likely breeding partners. Because males choose a clan at a mean age of 3.4 years, the number of likely breeding partners for a prospective philopatric male is reduced to females older than 3.4 years and younger than 5 years.

Although philopatric males chose clans containing fewer likely breeding partners, their fitness prospects were similar to those of

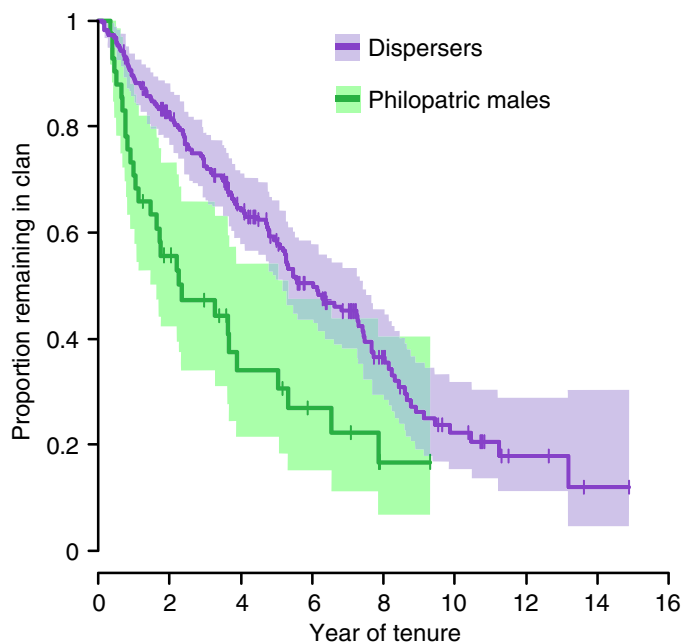


Fig. 5. Survivorship functions of the tenure of males in their first breeding clan. Curves correspond to the nonparametric Kaplan-Meier estimator of the proportion of philopatric males and dispersers with a total tenure longer than a given tenure. Data include complete tenures as exact values and tenures of males still alive at the end of the study as right-censored data (tick marks). Shaded areas represent 95% CIs.

dispersers. They sired fewer offspring than did dispersers with medium-ranking and low-ranking females, but because they occupied a high social rank throughout their tenure and social rank strongly increased reproductive success, they sired as many offspring as did dispersers. Moreover, as predicted, they started reproducing earlier than did dispersers and sired almost exclusively offspring with high-ranking females, a tactic that provides them with substantial short- and long-term fitness benefits because high-born offspring have a higher reproductive value than medium-born and low-born offspring; they survive better, benefit from “silver spoon” effects in terms of increased reproductive success, and contribute more to future generations than low-born offspring (29, 37). In our study population, after only eight generations, a large majority of the living adult population (82% of 340 adults with known female ancestor) were descendants of high-ranking females present at the beginning of the study [for a similar result on female descendants in a single hyena clan in the Maasai Mara in Kenya, see Holekamp *et al.* (38)]. We predicted that such fitness benefits should increase the propensity of males choosing their natal clan as their breeding group. Consistent with this prediction, twice as many males chose philopatry as expected if philopatry did not yield additional benefits compared to dispersal. The shorter tenure of philopatric males additionally suggests that males regularly assess their fitness prospects and disperse as a secondary breeding-group choice when the fitness advantages associated with their high social rank decrease. These findings demonstrate that, in spotted hyenas, the coexistence of philopatric males and dispersers results from a single, continuous process of breeding-group selection driven by the distribution of group qualities across natal and nonnatal groups and the fitness benefits associated

with the natal group. Our results are therefore consistent with a recent theoretical model that demonstrates that variation in dispersal distances among individuals of the same sex can emerge solely from the distribution and density of breeding partners when all individuals apply similar mate-based settlement rules (19).

Our results provide novel insights into the processes leading to philopatry and dispersal. By demonstrating that philopatric males can gain immediate, direct reproductive benefits, our study contrasts with most empirical studies on group-living mammals characterized by high dispersal biases. These studies reported that young philopatric males mainly gain indirect reproductive benefits through cooperative care of related offspring or delayed direct benefits after queuing for dominant breeder status (39–42). Most of these studies were conducted on male-dominated systems in which competition for females is high and access to high social rank and reproduction is correlated with male phenotypic traits such as age, body size, or fighting ability. We show here that in a promiscuous mating system, philopatry can provide similar fitness prospects to dispersal. Similar to systems where males and females are co-dominant (43), socially dominant hyena females can influence the competition among males and ensure, through social support (31), that their philopatric sons obtain a high social rank among sexually active males and its associated fitness benefits. These findings are consistent with the idea that fitness consequences of male philopatry depend on complex eco-evolutionary feedbacks and interactions between drivers of dispersal and male fitness, and the species’ social and breeding system (2, 5, 44).

Our findings on male reproductive success differ from those of a previous study on spotted hyenas in the Maasai Mara in Kenya, which reported that philopatric males were less successful than dispersers (32). They further contradict the suggestions that philopatric male hyenas undergo physiological suppression (45, 46) and are generally avoided by females as sires (32). These discrepancies may reflect real differences in hyena behavior and ecology between the two study populations, but they may also result from a difference in methodology. In contrast to our study, these previous studies used an age-based definition of philopatry, which resulted in the inclusion of males that were not yet sexually active and had not yet exercised breeding-clan choice (32, 34). Such a definition will likely bias estimates of male investment in reproduction and reproductive success in favor of dispersers [as discussed in Bercovitch (47) and Höner *et al.* (48)]. Our results highlight the importance and benefit of treating not only the dispersal movement but also the dispersal destination and philopatry as a choice of a breeding group or habitat. This implies that dispersal and philopatry should be carefully defined (9, 49), and the criteria applied should indicate reproductive investment (47, 48). It also requires a consideration of the quality of potential breeding sites, including the natal site (50, 51), and the identification of the ultimate and proximate factors driving male fitness. Only then will it be possible to assess whether differences in fitness and life history between philopatric individuals and dispersers result from differences in sexual maturity, their phenotype, the quality of the chosen breeding group, or the dispersal movement itself, and to understand the underlying processes leading to observed dispersal patterns (48, 50, 52–55).

Our study suggests that dispersal patterns within a sex may primarily depend on the likelihood that nonnatal groups provide higher fitness than the natal group, with the direction and magnitude of the bias depending on the nature of the drivers of individual fitness. In systems where the natal group systematically provides lower fitness than nonnatal groups,

leaving the natal group may be of high adaptive value and males may even emigrate without prior prospecting (56). This may drive the emergence of a dichotomous process of breeding-group selection in which individuals only choose between staying and emigrating, and of distinct philopatry and dispersal “syndromes” (4, 10, 56). By considering the quality of potential breeding groups, the choices of males, and the fitness outcome of their choices, we demonstrate that high dispersal biases can also emerge in systems in which natal groups can provide the highest fitness. We also demonstrate that philopatric males and dispersers may not necessarily represent two groups of individuals with distinct phenotypes and life histories. Our study illustrates the benefit of studying dispersal and philopatry within the broader framework of habitat selection theory to derive predictions on the causes and fitness consequences of breeding-group choices and dispersal patterns.

MATERIALS AND METHODS

Study design

All hyenas of the eight resident clans inhabiting the 250-km² floor of the Ngorongoro Crater (3°11'S, 35°34'E) in Tanzania were individually known and monitored between April 1996 and December 2014. Dispersal is strongly male-biased in this population, with approximately 85% of males leaving their natal clan and immigrating into another clan to breed, whereas females usually are philopatric (25, 57). The population is genetically linked to other hyena populations (58), but most males born in one of the Crater clans choose to breed in a Crater clan. During the study period, 41 Crater-born males started their reproductive career in their natal clan, and 213 males dispersed to another Crater clan. An additional 54 Crater-born males that reached 2.7 years, the mean age at clan choice minus 1 SD (see Results), either died or emigrated out of the Crater, and 24 males immigrated into Crater clans from elsewhere. Clans contained a mean number of 53.5 ± 5.5 adult (≥24 months old) members at the end of the study period.

Clan choice and quality of clans

We defined breeding-clan selection as the behavioral processes that result in a biased investment (a choice) in social relationships and sexual behavior that may influence an individual's survival and reproduction [adapted from “habitat selection” (10)]. We defined philopatry and natal dispersal as the outcome of breeding-clan selection that led a male to choose and start his reproductive career in his natal clan or in another clan, respectively. We considered a male to have chosen a clan when he expressed sexual behavior toward females and invested in joining the social hierarchy of sexually active males in the natal clan (“philopatric” male) or another clan (“disperser”) for at least 3 months (29). The date of clan choice was the date of first observation of such behavior for philopatric males and of first sighting in the new clan territory for dispersers, and defined the start of a male's tenure. We excluded males from the analyses that did not show any sign of sexual activity or had not met the 3-month criterion before their date of last sighting or the end of the study period.

We defined the quality of a breeding group as the social, demographic, and ecological characteristics of the group that influence the fitness of males, such as the number of unrelated breeding partners or competitors and food availability within the group territory [adapted from “habitat patch quality” (59)]. In spotted hyenas, male long-term fitness prospects and, thereby, clan quality are strongly influenced by

the number of likely female breeding partners as defined by female mate-choice rules (25).

Social rank

Social ranks were assigned on the basis of the outcome of dyadic interactions using submissive responses. To compare social rank within and between clans when clan size differed, adult females and sexually active males of a clan were assigned a standardized rank by distributing ranks evenly between the highest (standardized rank +1) and lowest rank (standardized rank -1) in the hierarchy of adult females and sexually active males, respectively (30). Individuals with standardized ranks within the top, middle, and lower thirds of the total range were classified as high-ranking, medium-ranking, and low-ranking, respectively. Maternal social rank was calculated when sons were 2 years of age. Male social rank was calculated at the start of each year of tenure in the chosen clan.

Paternity assignment and reproductive success of males

Female spotted hyenas produce litters of one or two (very rarely three) cubs with no distinct breeding season (33). We collected tissue, hair, and fecal epithelium from 1246 hyenas, including 1101 offspring born during the study period. Samples were stored in ethanol or dimethyl sulfoxide salt solution until DNA extraction. Fluorescent primers were used to amplify nine polymorphic microsatellite loci (60). The mean number of alleles per locus was 11.9 (range, 7 to 16), the mean expected heterozygosity was 0.83, the total exclusionary power was 0.999, and the error rate was 0.44% and set at 1.0%.

Paternities were assigned using maximum likelihood methods as implemented in CERVUS 3.0 (61). Candidate fathers were determined on the basis of conception dates, which were calculated by subtracting a gestation period of 110 days from birth dates estimated from pelage characteristics, body size, locomotory abilities, behavioral development and position, and the shape and size of the ears of cubs (62–64). All philopatric males and dispersers that were clan members when a litter was conceived were considered to be candidate fathers. For 1048 offspring (95.2% offspring sampled), all candidate males were genetically typed; the mean proportion of typed candidate males was 0.99. Extra-clan paternity was very rare; 1064 offspring (96.6% sampled) were sired by a philopatric or immigrant male of the clan. For the remaining 37 offspring, we performed a second analysis, which considered all adult males of the study population alive at conception as candidate fathers. For seven of these offspring (0.6% of all offspring), a male from another Crater clan was assigned paternity; for 30 offspring, no candidate male was assigned paternity at the 95% confidence level. To examine the influence of breeding-clan choice on male reproductive success, we restricted statistical analyses of reproductive success to offspring sired by philopatric males and dispersers with females from the chosen breeding clan. Male reproductive success was expressed as the annual number of offspring sired (“reproductive rate”) during each of the first 6 years of tenure. A period of tenure of 6 years covers a substantial period of the reproductive career of males in a clan (see Results). Statistical analyses were restricted to paternities assigned at the 95% confidence level.

Ethical statement

Our study was approved by the scientific advisory board of the Tanzania Wildlife Research Institute, the Tanzania Commission for Science and Technology, the Ngorongoro Conservation Area Authority, and the

Internal Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research in Berlin, the institute's equivalent of the Institutional Animal Care and Use Committee.

Statistical analyses

Statistical analyses were conducted using R software v.3.1.2 and associated packages (65). Data are means \pm SD unless stated otherwise. The threshold for significance was set to 5%. We tested predictions assuming that philopatric males and dispersers represented two groups of individuals applying distinct strategies in two steps: (i) direct comparison of raw data using nonparametric Mann-Whitney *U* tests to characterize differences in key traits of hyena life history between philopatric males and dispersers and (ii) ordinary least-squares LMs and GLMMs to identify the variables influencing these traits.

Age at clan choice and tenure at first reproduction

We conducted LMs to examine the factors influencing the age at which male hyenas chose their first breeding clan and the tenure at which they sired their first offspring. We included the identity of the natal clan as a categorical covariate (eight levels) to control for clan specifics that may affect male condition or age at sexual maturity and thereby influence the timing of male clan choice, such as the number of clan members and prey abundance. We included the identity of the chosen clan as a categorical covariate (eight levels) to control for factors that may influence the date of first observation of social or sexual behaviors toward members of the clan and first sighting of a male in the chosen clan's territory, such as our monitoring effort and territory size. For the analysis of the age at which males chose their first breeding clan, we applied a natural logarithm transformation to the dependent variable "age" (in years).

Annual reproductive rate

We conducted three GLMMs to examine factors influencing male annual reproductive rate. We used the annual number of offspring sired by males as the dependent variable (i) with females of all social ranks, (ii) with high-ranking females, and (iii) with medium- and low-ranking females. We used the natural logarithm as the link function and the Poisson distribution as the probability distribution of the dependent variable [package *lme4* v.1.1.7 (66)]. Covariates included male origin [that is, whether the male had grown up in the chosen breeding clan (native) or in another clan (foreigner)], male social rank, maternal social rank, the number of likely female breeding partners at clan choice, the year of tenure as the categorical variable (six levels), and the interaction between male origin and year of tenure; male identity was included as a random factor and assumed to follow a Gaussian distribution. Because male tenure was categorized in 1-year periods, GLMMs were restricted to males with complete years of tenure; a male was considered to have completed a year of tenure when all offspring conceived in the male's chosen clan and sampled during that period were genetically typed. The model on male annual reproductive rate with medium- and low-ranking females failed to fit the interaction between male origin and year of tenure because of very low variation in the reproductive rate of native males over tenure. We therefore recoded, for native males only, the six levels associated with the factor "year of tenure" as a single level termed "native_year," thereby constraining the effect of tenure on the reproductive rate of native males to be constant over tenure (see Fig. 3, C and D). Because this factor then corresponded to the combined effect of male origin, year of tenure, and their interaction, we reran the GLMM discard-

ing the covariate "male origin" to avoid redundant covariates. The recoding procedure allowed the model to compute regression coefficients separately for native males and foreigners; there is a single coefficient for native males and one coefficient for each of the six levels of years for foreigners (see table S5).

Regression coefficients for LMs and GLMMs were estimated by maximum likelihood using Laplace approximation (66). Significance of effects was assessed as the marginal contribution of each covariate to the full model by subtracting the likelihood of the reduced model without the specific covariate from the full model; *P* values were calculated using asymptotic LR tests [package *car* v.2.0.24 (67)] for LMs and parametric bootstrapped LR tests with 1000 simulations [package *pbkrtest* v.0.3.8 (68)] for GLMMs. Residuals of all LMs satisfied the assumptions of normal distribution [Lilliefors tests; package *nortest* v.1.0.2 (69)] and homogeneity of variances (residual plots). None of the GLMMs performed showed signs of overdispersion (Pearson residuals ratio), thereby conforming to the prerequisite for Poisson regressions or signs of multicollinearity between fixed effects (correlation matrices).

Male survival and tenure

Male survival and tenure were analyzed using the R package *survival* v. 2.37.7 (70). Differences in survival of philopatric males and dispersers after first clan choice were tested using Cox proportional hazards regressions with death or disappearance as the dependent variable. Individuals were considered to have died or disappeared when their dead body was found or when they were not sighted for at least 1 year. We assumed equal probability for both male categories to (re)disperse out of the Crater population. We used discrete time-event analysis on 1-year intervals to account for changes in male category (philopatric male versus disperser) over time and included males that were still alive at the end of the study (right-censored data). The assumption of proportional hazards over time was tested and validated using scaled Schoenfeld residuals. We compared male tenures in their first breeding clan using nonparametric Kaplan-Meier survivorship functions and the nonparametric log-rank test with (re)dispersal, death, or disappearance as the dependent variable, and tenures of males that were still alive and were still a member of their clan at the end of the study (right-censored data).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/3/e1501236/DC1>

Table S1. The age at which male spotted hyenas chose their first breeding clan as a function of male origin (native or foreigner), maternal social rank, and identities of natal and chosen clans.

Table S2. The tenure at which male spotted hyenas sired their first offspring as a function of male origin (native or foreigner), maternal social rank, the number of likely breeding partner at clan choice, and the identity of the chosen clan.

Table S3. The total number of offspring sired each year by male spotted hyenas as a function of male origin (native or foreigner), male social rank, maternal rank, the number of likely breeding partners at clan choice, year of tenure, and the interaction between male origin and year of tenure.

Table S4. The number of offspring of high-ranking females sired each year by male spotted hyenas as a function of male origin (native or foreigner), male social rank, maternal social rank, the number of likely breeding partners, year of tenure, and the interaction between male origin and year of tenure.

Table S5. The number of offspring of medium- and low-ranking females sired each year by male spotted hyenas as a function of the combined effect of male origin and year of tenure, male social rank, maternal social rank, and the number of likely breeding partners.

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Why do some males choose to breed at home when most other males disperse?

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