

# Dispersal Status Influences Hormones and Behavior in the Male Spotted Hyena

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Male spotted hyenas (*Crocota crocuta*) reach puberty at 24 months of age and then invariably emigrate from their natal clans 1 to 38 months later. Thus there are two classes of reproductively mature males in every *Crocota* clan: adult natal males born in the clan and adult immigrant males born elsewhere. In one free-living hyena population in Kenya, these two groups of males were compared with respect to measures of aggression, social dominance, sexual behavior, and circulating hormone levels. Adult natal males engaged in higher hourly rates of aggression than did immigrants, won all fights with immigrants, and were socially dominant to immigrants. In addition, adult natal males engaged in far lower hourly rates of sexual behavior with resident females than did immigrants, and natal males were never observed to copulate with natal females. Mean basal plasma cortisol values did not differ between the two groups of adult males, but cortisol concentrations in immigrants were positively correlated with tenure in the clan and with immigrant male social rank. Adult natal males had plasma testosterone levels significantly lower than those of immigrants. Social rank and plasma testosterone values were positively correlated among immigrant males. Thus two different relationships appear to exist between circulating testosterone and social rank in male *Crocota*: one apparent in immigrants and the other in natal adult males. Our results suggest that dispersal might disinhibit testosterone secretion in postpubertal male hyenas. © 1998 Academic Press

Natal dispersal, the complete and permanent departure of an individual from its original home area, is strongly male-biased in most mammals (Greenwood, 1980; Dobson, 1982; Stenseth and Lidicker, 1992). Before or shortly after puberty, male mammals usually

emigrate from their natal groups and join new social units. By contrast, female mammals are generally philopatric, and each female spends her entire life in the area and social group into which she was born. For gregarious mammals, dispersal represents one of the most profound and enduring environmental changes that an individual is ever likely to experience in its lifetime (Smale, Nunes, and Holekamp, 1997). At dispersal the animal moves to a new place, inhabited by unfamiliar conspecifics, in which it may have to learn to live by a new set of social rules. Here we investigate how a male's dispersal status affects circulating hormones and social behavior in the spotted hyena (*Crocota crocuta*).

Spotted hyenas are gregarious carnivores that live in social groups called clans. Each clan contains one to several matriline of adult females and their offspring, as well as one to several immigrant adult males. Clans are rigidly structured by hierarchical rank relationships (Kruuk, 1972; Tilson and Hamilton, 1984; Frank, 1986b; Mills, 1990; Holekamp and Smale 1990, 1993), and an individual's social rank determines its priority of access to food and other critical resources (Kruuk, 1972; Tilson and Hamilton, 1984; Frank, 1986b). Adult females are socially dominant to all adult males not born in the clan (Smale, Frank, and Holekamp, 1993; Smale *et al.*, 1997). Before cubs reach reproductive maturity they attain ranks in the clan's dominance hierarchy immediately below those of their mothers (Holekamp and Smale, 1993; Smale *et al.*, 1993). Individuals of both sexes maintain their maternal ranks as long as they remain in the natal clan (Smale *et al.*, 1993).

Female spotted hyenas are exposed early in development to unusually high levels of androgenic hormones, and females are heavily masculinized with respect to many aspects of their morphology and be-

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havior (Lindeque and Skinner, 1982; Glickman, Frank, Davidson, Smith, and Siiteri, 1987; Glickman, Licht, Frank, and Pavgi, 1992; Licht, Frank, Pavgi, Yalcinkaya, Siiteri, and Glickman, 1992). Nevertheless, dispersal behavior in *Crocuta* shows the normal pattern of mammalian sex differences: females typically spend their entire lives in their natal groups, whereas all males disperse from their natal clans between the ages of 24 and 62 months (Smale *et al.*, 1997; Mills, 1990; Frank 1986; Henschel and Skinner, 1987). Dispersal behavior in *Crocuta* is voluntary; males are not aggressively expelled from their natal clans, nor do males fall in social rank before dispersal (Smale *et al.*, 1997). In males of this species, plasma testosterone levels start to rise late in the second year of life (Glickman *et al.*, 1992), and males have viable sperm in their testes by 24 months of age (Matthews, 1939). Thus males may remain in their natal clan up to 38 months after puberty, and as a result, there are two classes of reproductively mature males in every *Crocuta* clan: natal males older than 24 months and immigrant males that have arrived from other clans. These two groups of adult males behave quite differently. Our purpose here is to compare adult natal and immigrant males with respect to agonistic behavior, sexual behavior, and plasma levels of testosterone (T) and cortisol.

## METHODS

The study site was the Talek area of the Masai Mara National Reserve, in southwest Kenya. This is an area of open, rolling grasslands grazed year round by large concentrations of several different ungulate species. The subject population was one large, stable *Crocuta* clan inhabiting a home range of approximately 60 km<sup>2</sup>. The boundaries of the study clan's home range have been stable at least since 1979 (Frank, 1986a). All hyenas in the study clan were known individually by their unique spots, and sex was determined from the dimorphic glans morphology of the erect phallus (Frank, Glickman, and Powch, 1990). From June 1988 through July 1997, observers monitored Talek hyenas 23 to 31 days per month except during April, 1991, when the animals were observed for only 14 days. Female *Crocuta* bear their litters in isolated natal dens and then transfer them to the clan's communal den when cubs are approximately 2 to 5 weeks old. When cubs were first observed above ground in the present study, at natal or communal dens, their ages were estimated to  $\pm 7$  days based on their pelage, size, and

other aspects of their appearance and behavior (e.g., folded ears, callous pads on carpals, motor coordination). Ages of all natal males were calculated on this basis. Because immigrant males originated in clans other than our study population, exact ages of immigrants were unknown. However, we determined relative ages of immigrant males based on height of the third lower premolar (PM<sub>3</sub>), as described by Kruuk (1972). In older animals, this specialized bone-crushing tooth is more heavily worn than it is in younger individuals. In addition, we recorded date of first appearance in the Talek home range of all immigrant males. Thus for these males we were able to measure ( $\pm 7$  days) time elapsed since immigration into the Talek clan, also called "tenure" in the Talek clan. As dependent variables in both natal and immigrant males, we monitored wins and losses in male-male agonistic interactions, hourly rates at which individual males directed aggression toward other adult males, hourly rates at which males directed sexual behavior toward resident adult females, and plasma hormone levels obtained from immobilized hyenas. The independent variable of interest was an adult male's dispersal status, determined strictly on the basis of whether he was observed or immobilized in his natal clan's home range or elsewhere.

**Behavioral observations.** Behavioral data for the analyses presented here were collected throughout the 5-year period from June, 1988, through June, 1993.

**Agonistic behavior.** Data documenting agonistic behavior represent critical-incident sampling (Altmann, 1974) of aggressive and appeasement behaviors observed in all social contexts. Aggression included the following behaviors: intention movement to bite, lunge, snap, bite, chase, displace, push, and stand over (Kruuk, 1972). Appeasement included the following behaviors: head-bob, carpal crawl, giggle, squeal, back off, and assumption of a body posture with the ears flattened back against the head, the tail between the legs, the body lowered and bent, and the head down (Kruuk, 1972). The "loser" in each agonistic interaction exhibited appeasement behavior in response to the "winner's" aggression. Outcomes of dyadic agonistic interactions among adult male hyenas were organized into a matrix based on the direction, not number, of interactions (Martin and Bateson, 1988), and social ranks were assigned on the basis of this matrix. By convention, the highest-ranking (alpha) individual was assigned a rank position of 1. An overall hourly rate of intrasexual aggressive behavior was calculated for each adult male by dividing the total number of observations in which a given male behaved aggres-

sively to other adult males by the total number of hours that the aggressor was observed in the presence of other adult males during the 5-year period. Mean hourly rates of intrasexual aggression were then compared for adult natal and adult immigrant males.

**Sexual behavior.** We recorded as critical incidents all occurrences of five different male sexual behaviors, described as follows. (1) Extended following: Here a male trails after an adult female, within 100 m of her, for 30 min to 3 h. We often find individual male-female pairs traveling like this alone, but it is also not uncommon to find a single adult female being trailed by five or six adult males. (2) Approach/avoid courtship display: Here a male first approaches within 1 m of a stationary (usually resting) female, where he halts, crosses his forelegs, and rubs his face against one foreleg ("bowing" behavior) before gingerly backing away from the female. This peculiar display appears to reflect the male's sexual interest in the female, but also his extreme ambivalence about approaching her within striking distance. (3) Participation in "baiting": During baiting behavior (Kruuk, 1972), males surround a female and take turns rushing in to nip at her flanks and hindquarters. The female crouches in the center, presumably to protect herself, but she often also darts out to target individual males with aggression. Participating males have their manes and tails erect and appear to be extremely excited. Although the exact function of this behavior pattern is unknown, the timing of its occurrence in relation to conception suggests that it may function as a form of noncopulatory sexual coercion by male hyenas (Szykman, Holekamp, and Smale, in review). (4) Mounting: Here the male places his forelegs on the female's back for a few seconds. (5) Copulation: While mounted, the male hops around behind the female until he can insert his erect phallus into her flaccid pseudopenis. Here the male remains mounted for up to 8 min.

**Immobilization procedure.** Between 1990 and 1997, 39 adult immigrant males and 17 natal males older than 24 months were anesthetized with Telazol (2.5 mg/kg body mass) administered in a lightweight plastic dart fired from an air rifle. All immobilizations took place between 0630 and 0800 h, when males were found resting. Within 10–17 min of dart impact, we drew a blood sample from each male's jugular vein into a heparinized Vacutainer tube. Using a cloth measuring tape, we then measured body length and leg length. Next, we used dial calipers to measure the length of one testis and the combined width of both testes. These two testis measurements were subsequently multiplied together to generate an estimate of

testis size. Finally, using dial calipers, we measured the height of the third lower premolar (PM<sub>3</sub>), as described by Kruuk (1972). Males typically recovered from anesthesia within 60 min. All immobilizations were performed in accordance with Kenyan law and with NIH animal treatment guidelines.

**Hormone assays.** Blood samples were centrifuged immediately after darting. Plasma was drawn off and stored in LN<sub>2</sub> until transported on dry ice to the United States, where plasma was stored at  $-80^{\circ}\text{C}$  until assay. Aliquots of plasma from each male were assayed for total testosterone (T) and cortisol using coated tube <sup>125</sup>I kits obtained from Diagnostic Products Corp. (Los Angeles, CA). Both kits were validated for use with this species by demonstrating parallelism between serial dilutions of plain and spiked *Crocota* plasma and the standard curves generated with kit calibrators. Detection limits for T and cortisol assays were 0.04 ng/ml and 0.2  $\mu\text{g/dL}$ , respectively. Cross-reactivity of the T antiserum with 5- $\alpha$ -dihydrotestosterone was 3.3% and was less than 0.10% with any other androgen. Cross-reactivity of the cortisol antiserum was less than 1.0% with any other naturally occurring steroid hormone. The mean coefficient of variation between T assays ( $N = 7$ ) was 7.1% and between cortisol assays ( $N = 3$ ) was 5.2%. The mean coefficient of variation for high and low control tubes run within each T assay was 6.8% and within cortisol assays was 4.3%.

**Statistical analysis.** Mean hourly behavior rates, body size measures, and hormone levels were compared in natal and immigrant males using Student's *t* tests. In addition, correlation coefficients (Pearson's *R*) were obtained to indicate whether specific measurements varied with natal male age, immigrant tooth wear, or with immigrant tenure in the Talek clan. Spearman's *R* was used as the correlation coefficient when rank based on age or dominance status was involved as an independent variable in any analysis. The statistical significance of relationships between variables was evaluated using analysis of variance (ANOVA). Mean values were presented  $\pm\text{SE}$ , and differences between groups were considered statistically significant when  $P < 0.05$ .

## RESULTS

**Agonistic behavior.** Fifteen natal males older than 24 months were observed to interact with 12 immigrant males in 831 agonistic interactions between 1988 and 1993 (Table 1). Without exception, adult natal

### Outcomes of Agonistic Interactions among Adult Males Present in the Talek Clan from June, 1988, through May, 1993

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*Note.* Males are listed on the left vertical axis as winners in these interactions and along the top horizontal axis as losers. The male listed at the top of the winners column is the highest ranking, and the male listed at the bottom is the lowest ranking of those included here. Each number in the matrix represents the number of agonistic interactions observed between members of each male dyad in which the loser appeased the winner. Only those adult natal males observed interacting with adult immigrant males were included here, as were only those immigrants observed to interact with adult natal males. Adult natal males appear in regular type, and immigrants appear in boldface type. Ranks of adult natal males are isomorphic with the social ranks of their mothers. Among immigrants, male rank is strongly correlated with tenure in the Talek clan, such that male "4" arrived first and male "ZI" arrived last.

males were the winners in these fights, and immigrant males were the losers. Although outcomes of 13 of 831 fights (1.6%) were inconsistent with the dominance rankings shown in Table 1, these occurred only either in fights between two immigrants ( $N = 2$ ) or in fights between two natal adult males ( $N = 11$ ). Dominance rankings among natal males were almost perfectly isomorphic with the social ranks of their mothers, as described previously (Holekamp and Smale, 1993; Smale *et al.*, 1993). Dominance rankings among immigrant males were unrelated to age ranks of immigrants based on tooth wear ( $R_s = 0.146$ ;  $F = 0.182$ ;  $df = 1, 18$ ;  $P = 0.681$ ), but were highly correlated with immigrant tenure in the Talek clan ( $R_s = 0.982$ ;  $P < 0.001$ ): the highest-ranking immigrants had been present in the Talek home range for the greatest num-

ber of months, as described by Smale *et al.* (1997). Immigrant males were only able to dominate other adult immigrants who arrived later in the Talek clan. Finally, adult natal males directed aggressive behavior at other adult males at hourly rates over six times as high as rates observed for immigrant males (natal males  $\bar{X} = 1.34 \pm 0.09$  aggressions per hour; immigrant males  $\bar{X} = 0.22 \pm 0.01$  aggressions per hour;  $t = 2.886$ ,  $df = 45$ ;  $P = 0.008$ ). Thus adult natal males were significantly more aggressive toward other adult males than were immigrants, were socially dominant to all immigrants, and were the winners of all fights with immigrants. Hourly rates of intrasexual aggression were not correlated with maternal rank among adult natal males ( $R_s = -0.073$ ;  $F = 0.468$ ;  $P = 0.506$ ), nor were aggression rates correlated with tenure

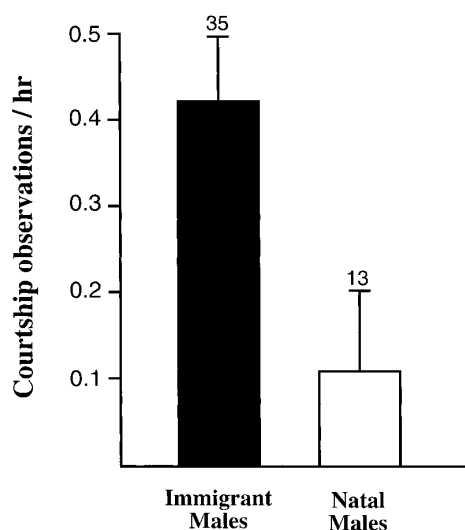


FIG. 1. Mean hourly rates at which adult natal and immigrant males directed sexual behavior toward adult resident females of the Talek clan. Sample sizes represent numbers of individuals sampled. Data are expressed as means  $\pm$  SEM.

among immigrants ( $R_s = -0.409$ ;  $F = 0.942$ ;  $P = 0.355$ ).

**Sexual behavior.** From 1988 through 1993, we observed 581 incidents of male sexual behavior in our study area. Except where noted in the following analyses, all five monitored types of male sexual behavior were treated together. During this 5-year period, 19 natal males reached 24 months of age and then remained in the study area for at least another 6 months. Of these 19 natal adult males, 13 (68%) directed sexual behavior toward adult resident females. However, whereas 30% (13 of 43) of adult males resident in the clan from 1988 through 1993 were natal adult males, they accounted for only 12% (70 of 581) of the observed courtship interactions with females. Thus the participation of natal males in sexual interactions with resident females was less than half as great as their representation in the population would have predicted had natal and immigrant males been behaving similarly. The mean hourly rate at which adult natal males exhibited courtship behavior was only about one-fourth as high as the mean rate observed for immigrant males (Fig. 1:  $t = 2.138$ ;  $df = 45$ ;  $P = 0.039$ ). Although natal adult males were observed to mount resident females, no natal males ever participated in any of the 16 complete copulations observed during this 5-year period or, in fact, in any of the 24 copulations we observed in the Talek clan between 1988 and 1998. Thus, although postpubertal natal males courted and baited resident females, and even mounted them,

they were never observed to copulate with resident females and their sexual motivation generally appeared to be less than that exhibited by immigrant males interacting with the same adult females.

**Tooth wear.** Although an immigrant's tenure in the Talek clan was highly correlated with his social rank relative to those of other immigrants, we found no significant relationship between PM<sub>3</sub> height in immigrants and their tenure in the Talek clan ( $R_p = -0.431$ ;  $F = 1.78$ ;  $df = 28,9$ ;  $P = 0.177$ ), suggesting that an immigrant's relative age was a good predictor of neither his tenure in his new clan nor his social rank in the new clan. Mean PM<sub>3</sub> height in immigrant males was less than that measured in adult natal males indicating that, on average, immigrants were older than adult natal males (immigrants:  $\bar{X} = 16.34 \pm 0.10$  mm vs natal males  $\bar{X} = 18.13 \pm 0.12$  mm;  $t = -2.73$ ;  $df = 40$ ;  $P = 0.01$ ). This is not surprising considering that adult natal males had not yet dispersed, whereas immigrants might have been dispersed for several months or years at the time PM<sub>3</sub> height was measured. However, PM<sub>3</sub> height in all adult natal males was within the immigrant range (immigrants 10.4–20.8 mm vs natal males 16.2–20.1 mm). Thus, although adult natal males appeared to be younger, on average, than immigrants, their tooth wear patterns indicated that natal males were fully adult. Nevertheless, in order to evaluate adult natal and immigrant males of comparable ages, we excluded the youngest adult natal males and the oldest immigrants in all of the analyses presented below, except where otherwise indicated. That is, we restricted the following analyses to 12 (of 17) natal males whose PM<sub>3</sub> height fell within one standard deviation of the immigrant mean and 30 (of 39) immigrant males whose PM<sub>3</sub> height fell within the range (16.2–20.1 mm) obtained for adult natal males. In these subgroups, mean PM<sub>3</sub> height for adult natal males ( $\bar{X} = 17.93 \pm 0.36$ ) did not differ significantly from the mean value for immigrants ( $\bar{X} = 17.41 \pm 0.28$ ;  $t = -1.56$ ,  $df = 40$ ;  $P = 0.131$ ).

**Hormone and size measurements obtained during immobilizations.** Although mean testis size did not differ between adult natal and immigrant males (Table 2;  $t = -0.943$ ;  $df = 40$ ;  $P = 0.352$ ), plasma T levels were significantly higher in immigrants than in natal males (Fig. 2A;  $t = 3.37$ ;  $df = 40$ ;  $P = 0.029$ ). To determine whether this difference in T levels might be due to maturational variables rather than effects of dispersal status, we compared the two groups of males with respect to the body size measures obtained when males were anesthetized. Adult natal and immigrant males were statistically indistinguishable by these

**TABLE 2**

Body Measurements (in mm) Compared for Adult Natal and Immigrant Male Hyenas

Measurement (mm)	Adult immigrant males (N = 30)	Adult natal males (N = 12)	P value
Testis length $\times$ testis width	940 $\pm$ 57	1030 $\pm$ 86	0.352
Body length	96 $\pm$ 2	95 $\pm$ 9	0.666
Leg length	97 $\pm$ 1	96 $\pm$ 1	0.339

Note. Means are given  $\pm$  SEM, and *P* values were derived using Student's *t* tests (see text).

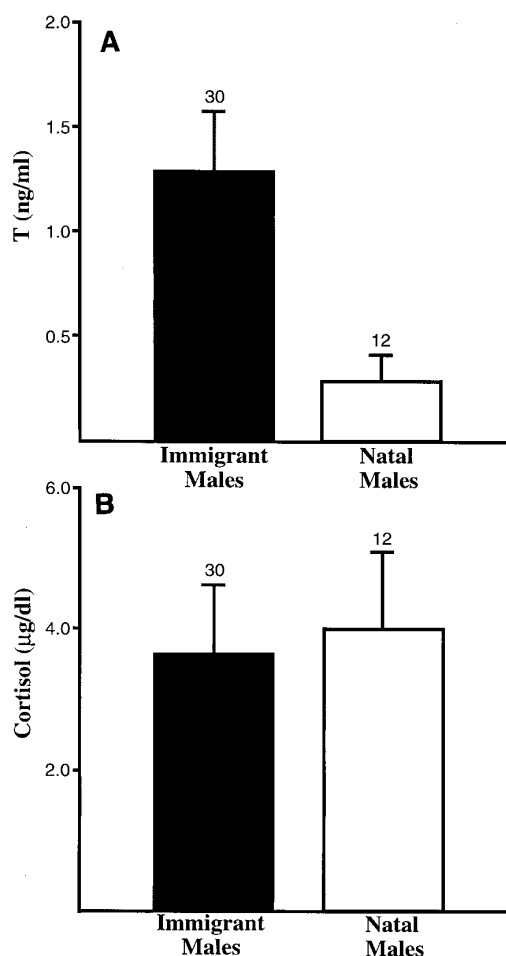
measures. Neither body length ( $t = 0.435$ ;  $df = 40$ ;  $P = 0.666$ ) nor leg length ( $t = 0.970$ ;  $df = 40$ ;  $P = 0.339$ ) was greater among immigrants than among adult natal males (Table 2). Testis size was correlated neither with tenure among immigrants (Fig. 3A;  $R_p = -0.346$ ;  $F = 0.317$ ;  $df = 1,28$ ;  $P = 0.578$ ) nor with age among adult natal males (Fig. 3B;  $R_p = -0.265$ ;  $F = 1.208$ ;  $df = 1,10$ ;  $P = 0.297$ ). Thus, since all males sampled were reproductively mature, within the same age range, and indistinguishable on the basis of morphological measures, it appeared that dispersal status rather than age accounted for the significant difference we observed in plasma T levels between natal males and immigrants.

Plasma cortisol levels did not differ between natal and immigrant males (Fig. 2B;  $t = -0.171$ ;  $df = 40$ ;  $P = 0.865$ ), so the difference observed in plasma T levels did not appear to be mediated by glucocorticoids. Plasma cortisol levels increased significantly with immigrant male tenure (Fig. 4A;  $R_p = 0.216$ ;  $F = 7.334$ ;  $df = 1,28$ ;  $P = 0.011$ ), but not with either immigrant  $PM_3$  wear ( $R_p = -0.200$ ;  $F = 5.475$ ;  $df = 28,1$ ;  $P = 0.106$ ) or natal male age (Fig. 4B;  $R_p = 0.122$ ;  $F = 0.669$ ;  $df = 1,10$ ;  $P = 0.432$ ).

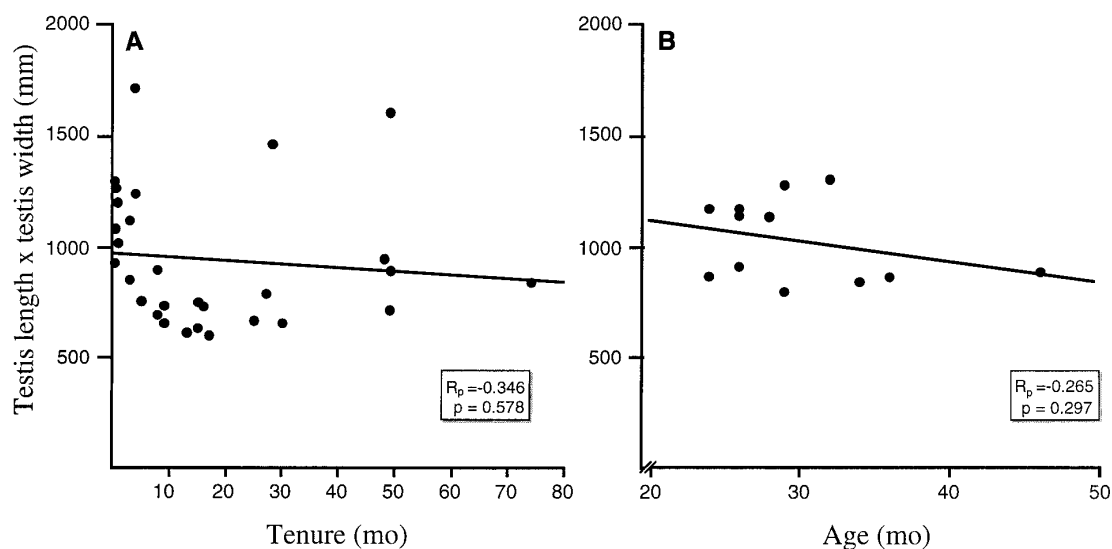
Finally, we attempted to ascertain whether higher circulating T in immigrants was implicated as either a cause or a consequence of dispersal behavior. Among all sampled immigrant males, plasma T levels increased significantly with tenure in the Talek clan (Fig. 5A;  $R_p = 0.335$ ;  $F = 7.254$ ;  $df = 1,34$ ;  $P = 0.012$ ), but not with  $PM_3$  wear ( $R_p = -0.553$ ;  $F = 0.242$ ;  $df = 1,34$ ;  $P = 0.948$ ). Two immigrant males were immobilized again 2 and 5 years, respectively, after their first dartings in the Talek home range. Plasma T levels in both these males increased dramatically between immobilizations: one from 0.05 to 5.33 ng/ml and the other from 0.29 to 4.88 ng/ml.

Among adult natal males, plasma T levels did not vary significantly with age (Fig. 5B;  $R_p = -0.253$ ;  $F =$

0.500;  $df = 1,10$ ;  $P = 0.496$ ). Furthermore, two natal males were immobilized twice after they were 24 months of age, but before they dispersed. Their plasma T levels were 0.38 and 0.00 ng/ml in their first samples and 0.00 and 0.28, respectively, in their second samples. Thus increasing age did not necessarily lead to an increase in plasma T levels in adult natal males. Finally, five natal males were sampled as adults both before and after they dispersed. Their mean plasma T levels increased from 0.23 ng/ml before dispersal to 1.53 ng/ml after dispersal ( $t = -3.601$ ;  $df = 4$ ;  $P = 0.023$ ). Thus it appeared not only that dispersal status influenced the behavior of adult males, but also that it affected their plasma T levels as well.



**FIG. 2.** Comparison of immigrant and adult natal male hyenas with respect to plasma levels of (A) testosterone and (B) cortisol. Sample sizes represent numbers of individuals sampled. Data are expressed as means  $\pm$  SEM.

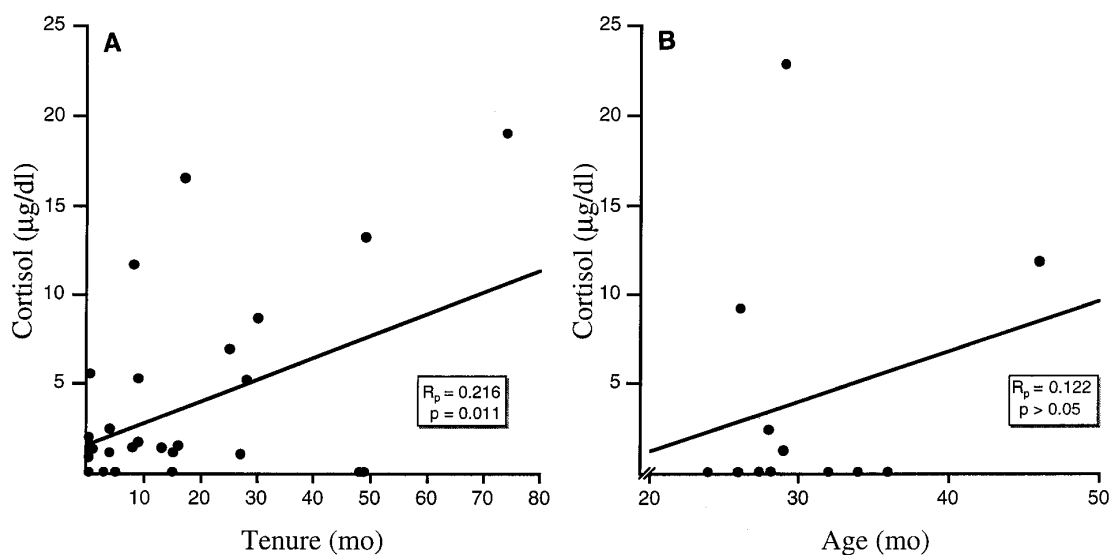


**FIG. 3.** Testis size in (A) immigrant males as a function of months since arrival in the Talek clan and (B) adult natal males as a function of age.

## DISCUSSION

The simple act of moving across the invisible boundary of the natal clan's home range apparently has profound consequences with respect to both social behavior and endocrinology in the male spotted hyena. When males leave their natal clans, they behave submissively to all new hyenas encountered, and this is the point during ontogenetic development at which

females come to dominate males (Smale *et al.*, 1993). Unlike some primates in which male social rank typically increases after dispersal (e.g., Hamilton and Bulger, 1990), the social rank of male *Crocota* inevitably declines when they leave the natal clan (Smale *et al.*, 1997). Male hyenas often remain in their natal clans until long after they have reached adult body size and become reproductively mature. These adult natal males are socially dominant to all immigrants, exhibit



**FIG. 4.** Plasma cortisol values in (A) immigrant males as a function of months since arrival in the Talek clan and (B) adult natal males as a function of age.

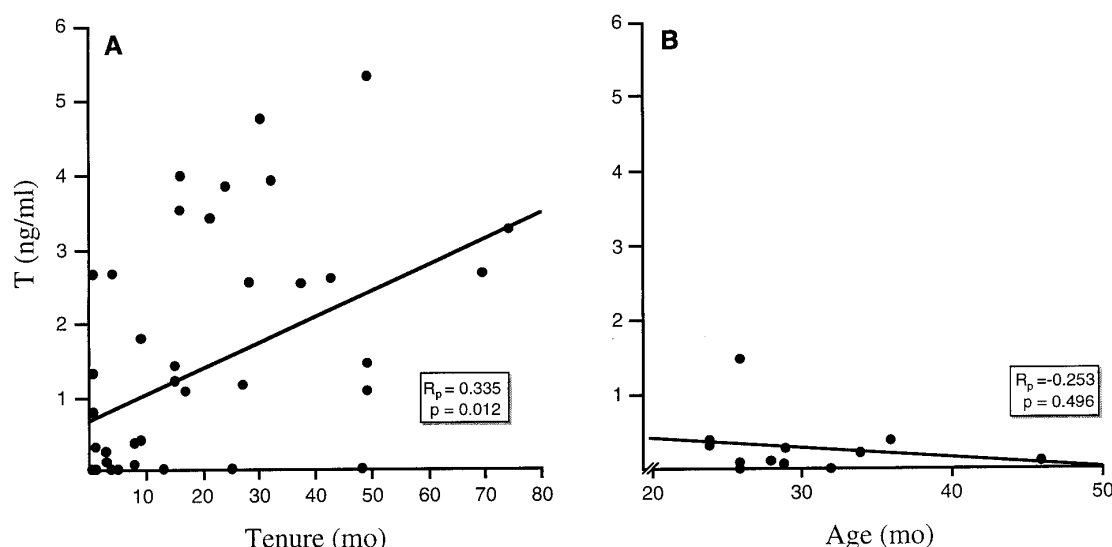


FIG. 5. Plasma T values in (A) immigrant males as a function of months since arrival in the Talek clan and (B) adult natal males as a function of age.

higher hourly rates of aggression, and inevitably win in all their agonistic interactions with immigrant males, yet their plasma T levels are far lower than are those measured in immigrants. These results thus stand in striking contrast to those presented by many earlier workers studying male lizards (e.g., Denardo and Sinervo, 1996), birds (e.g., Wingfield, Ball, Dufty, Hegner, and Ramenofsky, 1987), rodents (e.g., Bronson and Eleftheriou, 1965; Lloyd, 1971; Gaines, Fugate, Johnson, Johnson, Hisey, and Quadagno, 1985; Huhman, Moore, Ferris, Mougey, and Meyerhoff, 1991), lagomorphs (Farabollini, 1987), carnivores (e.g., Creel, Creel, Mills, and Monfort, 1997), ungulates (Lincoln, Guinness, and Short, 1972), nonhuman primates (e.g., Rose, Holaday, and Bernstein, 1971; Rose, Gordon, and Bernstein, 1972; Bernstein, Rose, and Gordon, 1974; Bernstein, Gordon, and Rose, 1983; Sapolsky, 1982; Coe, Smith, Mendoza, and Levine, 1983; Eberhart, Keverne, and Meller, 1983; Steklis, Brammer, Raleigh, and McGuire, 1985), and humans (e.g., McCaul, Gladue, and Joppa, 1992; Booth, Shelley, Mazur, Tharp, and Kittok, 1989; Mazur and Lamb, 1980). In all of these taxa, winners in fights or competitions have higher T levels than do losers, and more aggressive individuals have higher T levels than do less aggressive conspecifics. Only the positive relationship between dominance and T observed among immigrant male hyenas was consistent with the pattern seen in the myriad taxa listed above.

Frank, Davidson, and Smith (1985) found that "resident" male *Crocota* had higher plasma T levels than

did "transient" males, but it is difficult to compare data presented by these earlier investigators with our own because they did not distinguish adult natal males from immigrants. Van Jaarsveld and Skinner (1991) divided male hyenas into three categories and found that both "resident natal males" and "peripheral immigrant males" had significantly lower T levels than did "central immigrant males." These investigators did not attempt to compare natal and immigrant males with respect to age or tooth wear. However, since peripheral immigrants had dispersed more recently than had central immigrants (Henschel and Skinner, 1987), these earlier findings were consistent with our conclusion here that immigrant males present in the study clan for longer periods of time had higher plasma T than did either immigrants with shorter tenure or adult natal males.

Woodroffe, Macdonald, and da Silva (1993) found that immigrant male European badgers (*Meles meles*) had higher blood titers of T than did resident males, even though testis size in the two groups of males did not differ. However, immigrant males were larger and older than were resident males, so effects on T of age and dispersal status could not be separated effectively in badgers. In male *Crocota*, however, we found significantly higher T levels in immigrant males even after we had controlled for age. Thus, in postpubertal male spotted hyenas, dispersal status appeared to influence plasma T levels more strongly than did age.

Although we found that basal plasma cortisol values did not differ between natal males and immi-



grants, we did find that cortisol levels were positively correlated with social rank among immigrants. Thus, with respect to the relationship between plasma cortisol levels and social rank, immigrant male hyenas more closely resemble some populations of monkeys and Cape hunting dogs (*Lycaon pictus*) in which dominant individuals have higher glucocorticoid levels than do subordinates (McGuire, Brammer, and Raleigh, 1986; Coe *et al.*, 1983; Creel *et al.*, 1997; Creel, Creel, and Monfort, 1996, but see Steklis *et al.*, 1985; de Villiers, van Jaarsveld, Meltzer, and Richardson, 1997). Perhaps glucocorticoid levels increase in immigrant male hyenas over time in their new clans because males with longer tenure attempt to interact more frequently with aggressive resident females than do newly arrived immigrants. In any case, low social rank among male *Crocota* is not associated with physiological indicators of prolonged stress as occurs in various other mammals [e.g., pigs (Fernandez, Muenier-Salaun, and Mormede, 1994); hamsters (Huhman *et al.*, 1991); baboons (Sapolsky, 1982); and mice (Bronson and Eleftheriou, 1965; Louch and Higgenbotham, 1967)].

When both classes of adult male hyenas were considered together, it was clear that the higher-ranking, more aggressive adult natal males had lower plasma T levels than did the lower-ranking and less aggressive immigrants. However, when immigrant males were considered alone, we found the opposite relationship between dominance and plasma T levels. We suggest three hypotheses germane to these contrasting relationships that might explain why immigrant males have higher T levels than do the higher-ranking adult natal males. These three hypotheses are not mutually exclusive. First, it is possible that immigrant males do not perceive adult natal males as salient "challengers" (*sensu* Wingfield, 1984; Wingfield *et al.*, 1987) in intra-sexual competition for access to resident females. This is suggested, for example, by the observation that the sexual ardor exhibited by adult natal male hyenas was significantly less intense than was that exhibited by immigrants. Among male passerine birds, Wingfield *et al.* (1987) have found that T levels are correlated with aggression only in response to perceived threats. If immigrant male hyenas do not perceive adult natal males as viable challengers during competition for mates, then the higher social status of natal males in the clan's overall hierarchy may have no inhibitory effect on hormone secretion among immigrants.

Second, perhaps exposure to novel or sexually receptive females in the new clan has a major stimulatory effect on T secretion in immigrant males. Given

the masculine genital morphology of the female spotted hyena, coercive male behavior during copulation is impossible, so female mate choice determines which adult males father cubs. If resident females prefer immigrants over adult natal males as mates, then dispersal should increase the probability that a male will be selected as a mate by resident females in his new clan. Previous workers have found that plasma T levels rise in male rabbits, mice, rats, elephants, monkeys, rams, and bulls, either following copulation or after visual exposure to novel, receptive females (Rose *et al.*, 1972; Macrides, Bartke, and Dalterio, 1975; Saginor and Horton, 1968; Haltmeyer and Eik-Nes, 1969; Katongole, Naftolin, and Short, 1971; Jainudeen, Katongole, and Short, 1972; Purvis and Haynes, 1974; Sanford, Palmer, and Howland, 1974). Similarly, exposure to novel or sexually receptive females may stimulate T secretion in immigrant male hyenas. Interestingly, exposure to unfamiliar males stimulates ovarian activity in some female mammals (e.g., rodents: reviewed in Bronson, 1989; tamarins, *Saguinus oedipus*: Widowski, Porter, Ziegler, and Snowdon, 1992), suggesting functional parallels to the stimulatory effects on males of novel or receptive females.

A third possibility is that persistent exposure to female kin in the natal area inhibits T secretion in adult natal male hyenas and that dispersal disinhibits T secretion. French and Schaffner (1995) found that breeding male marmosets (*Callithrix kuhli*) had higher urinary T than did adult males still living in their natal groups. T levels in the latter rose significantly when adult sons were removed from their family groups and housed either in isosexual groups or with an unrelated adult female. Like our results from free-living spotted hyenas, the marmoset findings suggest that removal of a male from the presence of kin might disinhibit T secretion. Postpubertal natal male pied kingfishers copulate less and have lower T levels than do immigrant males (Reyer, Dittami, and Hall, 1986). A comparable phenomenon has been described in postpubertal female tamarins, which fail to ovulate while housed with mothers or brothers, but ovulate shortly after pairing with novel males (Widowski, Ziegler, Elowson, and Snowdon, 1990). Thus inhibitory effects on gonadal hormone levels of persistent exposure to kin may operate broadly in gregarious vertebrates of both sexes.

Because our study was largely correlational, we cannot rule out the possibility that endocrine factors cause male dispersal in the spotted hyena. Our only hints about directionality in the relationship between T and dispersal derive from our comparison of plasma T in

adult natal males before and after they dispersed. In these males, T levels were significantly lower before than after dispersal, suggesting that elevated T does not activate (Phoenix, Goy, Gerrall, and Young, 1959) dispersal behavior in *Crocota*. Holekamp, Smale, Simpson, and Holekamp (1984) evaluated possible activational effects of T on natal dispersal behavior in Belding's ground squirrels (*Spermophilus beldingi*), another mammalian species in which all males inevitably disperse. Castration of male squirrels at weaning did not keep them from dispersing a few weeks later. Interestingly, however, perinatal T treatment has been found to organize male dispersal behavior in Belding's ground squirrels (Nunes and Holekamp, in review). Similarly, although it appears unlikely that T activates male dispersal in *Crocota*, it is certainly possible that T organizes this behavior pattern, which appears to have such profound consequences for male reproductive success. Finally, although the probability of dispersal by Belding's ground squirrels is determined by perinatal exposure to T, the timing of dispersal in that species is determined by interaction between available energy stored as fat and endogenous circannual timing mechanisms (Nunes, Ha, Garrett, Muecke, Smale, and Holekamp, 1998). Similarly, nonendocrine physiological variables might influence the timing of dispersal behavior among male spotted hyenas.

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