Testosterone Manipulation of Male Attractiveness has no Detectable Effect on Female Home-Range Size and Behavior During the Fertile Period

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Abstract

Female dark-eyed juncos (*Junco hyemalis*) are socially monogamous, but they engage in extra-pair copulations (EPCs). We examined spatial activity and behavior of female juncos during their fertile period to determine whether they engaged in tactics likely to facilitate EPCs and whether any such tactics varied with the attractiveness of their social mates. We manipulated the attractiveness of social mates by implanting experimental males with tubes containing testosterone (T-males) and control males with empty tubes (C-males). Previous findings in free-living juncos showed that females mated to C-males were more likely to produce extra-pair young than females mated to T-males. We radio-tracked 13 females (eight C-mated, five T-mated) for an average of 15 h each over 3 d during their fertile periods. We predicted that C-mated females, to compensate for the induced relative unattractiveness of their social mates, would foray from their territories to seek EPCs and as a result would have larger home ranges than T-mated females. Females of both treatment groups made extra-territorial forays, some of considerable distances, but we observed no EPCs during forays. Further, neighboring T- and C-males frequently made incursions into the home ranges of T- and C-mated females but we saw no EPCs during these incursions. Our ability to detect statistical differences was limited by sample size, but given that constraint, we found no detectable difference in female home-range size in relation to the treatment of their mates, nor did other female behavior differ according to male treatment. Male behavior was significantly affected by testosterone treatment. C-males guarded their mates more closely than did T-males. We conclude that female juncos make extra-territorial movements during their fertile period without regard to male attractiveness (testosterone treatment), but we found no evidence that these function as a special tactic to gain EPCs.

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Introduction

Copulations outside the pair bond [i.e., extra-pair copulations (EPCs)] are common in many temperate-zone socially monogamous songbirds (Birkhead and Møller 1992). Studies of genetic relatedness employing molecular methods have shown that EPCs are often successful: in a variety of species 20–40% of females typically produce young sired via extra-pair fertilizations (EPFs) (Stutchbury and Morton 1995; Westneat and Sherman 1997). Originally, researchers focused on possible advantages that extra-pair matings might confer on males (Westneat 1987; Morton et al. 1990) and rarely considered that females might also gain advantages. The view that EPCs benefited only males was based on the observation that many EPCs appear forced, because they are often preceded by intersexual chases and aggression. However, this interpretation is complicated by the fact that females may resist a male's attempt to copulate as a "ploy" to test his quality (e.g. Cox and Le Boeuf 1977; Wagner 1991; Hoi 1997). Recent evidence indicates that females play a larger role in determining the identity of extra-pair mates than was formerly recognized (reviewed in Stutchbury and Neudorf 1997).

The fact that in most bird species copulations cannot be forced (Fitch and Shugart 1984), coupled with observations that some females may actively seek EPCs, suggests that females may gain benefits from participating in them and may cooperate with males. Advantages proposed for females (reviewed in Westneat et al. 1990) include insurance against infertility of the social mate (Wetton and Parkin 1991), material benefits such as access to food or more effective nest defense (e.g. Gray 1997), and 'good genes' for the offspring (Hamilton 1990). Studies have identified certain male phenotypic traits that correlate with male EPF success and that thus may be indicative of male quality, such as larger song repertoires (Hasselquist et al. 1996) or higher social rank (Otter et al. 1994). Whether traits preferred by females reflect differences in male fertility, parental ability, or resource holding power, or quality of genes remains to be determined (e.g. Sheldon 1994a). These potential benefits are not necessarily mutually exclusive and may also vary among species.

To better understand whether females play a role in determining which males sire their offspring, it is necessary to study behaviors that result in EPCs. Females of other species employ at least two tactics: (1) active pursuit of EPCs by leaving the social mate's territory (e.g. Wagner 1991; Kempenaers et al. 1992; Double and Cockburn 2000), and (2) attraction of extra-pair males to the social male's territory by advertising their fertility (e.g. Montgomerie and Thornhill 1989; Sheldon 1994b; Hoi 1997). Females in some species may use both tactics (Neudorf 1996; Neudorf et al. 1997), but neither may be effective when interactions among males limit female opportunity to engage in them (Wagner 1996).

We asked whether either tactic is employed by female dark-eyed juncos (*Junco hyemalis*). The junco is a good species in which to study tactics facilitating EPCs, which in this species are common: over 34% of nests on our study area contain extra-pair young (Ketterson et al. 1997). Females that copulate with more than one male have greater reproductive success, suggesting that EPCs are beneficial to these females (Ketterson et al. 1997). Furthermore, in juncos it is possible to alter experimentally the number of EPFs a male obtains. Males whose testosterone levels are artificially enhanced and then released to breed have greater EPF success (Raouf et al. 1997), but whether this difference is a result of male behavior or female behavior is not known. In captive juncos in which females were permitted to freely choose between two males, they preferred to associate with T-males over C-males (Enstrom et al. 1997).

We reasoned that the female preference for T-males observed in captive birds might also be expressed in free-living juncos and, if so, that females socially mated to T-males would be less likely to engage in behaviors likely to result in EPCs. We asked whether the spatial or other behavior of T- and C-mated fertile females differed. We used radio-tracking to follow females and to detect forays off territory, and we quantified female behaviors, including vocalizations that might function in a way to attract potential extra-pair mates. We predicted that T-mated females would be less likely than C-mated females to make forays onto the territories of neighboring males and/or to behave conspicuously in ways that advertise the fact that they are fertile.

Methods

Study Area and Species

We conducted our research between April and July 1998 and 1999, at the University of Virginia's Mountain Lake Biological Station (hereafter MLBS) in Giles County, Virginia (37°22′N, 80°32′W). The habitat is montane deciduous forest and forest edge, at an elevation of 1000–1330 m (see Chandler et al. 1994 for details). The junco there is the Appalachian subspecies, *J.h. carolinensis*, a nearly sedentary population in which breeding males begin to defend all-purpose territories in early to mid-April. Juncos are socially monogamous, and both males and females feed offspring.

Between April 15 and May 15 we captured males and females in baited mist nets and potter traps, individually color-banded each, and implanted about 100 males subcutaneously with two- 10-mm long capsules of medical grade silastic tubing either filled with crystalline testosterone (T-males) or empty (C-males). This treatment maintains testosterone levels of T-males at the natural spring maximum throughout the breeding season (Ketterson et al. 1992, 1996, 2001), whereas in nature C-males' testosterone levels decline after males establish territories and obtain a social mate.

Radio-tracking

Radio-tracking has been used successfully to monitor continuous movements of male juncos at MLBS (Chandler et al. 1994, 1997), and it proved equally effective for females. We used BD2A transmitters (Holohil Systems Ltd., Woodlawn, Ontario, Canada), with a range of 200–300 m on our study area. Transmitters were attached via a leg-loop harness (modified from Rappole and Tipton 1991; see also Neudorf et al. 1997; Smulders et al. 2000), which together weighed 0.8 g, or 4–5% of female body mass. We also put transmitters on six males to monitor their locations with respect to their mates. We used TRX 1000-S receivers and three-element Yagi antennas (Wildlife Materials Inc., Carbondale, IL, USA).

Female fertile period

We captured and radio-tagged 10 females just before or just after they began to build nests; three additional females that we caught during early incubation were immediately deprived of their eggs (simulated predation) which caused them to renest. We conservatively estimate that a female junco's fertile stage lasts from the initiation of nest-building until the day she lays the penultimate egg (Birkhead and Møller 1992). Before we tracked any female, we allowed her at least 24 to acclimate to the radio transmitter.

Female behavior during tracking

We tracked each female during four tracking periods on several days: dawn: 0600–0830, morning: 0900–1200, afternoon: 1400–1700 and dusk: 1830–2100 hours. We attempted to accumulate a total of 16 h for each female over the four tracking periods, with at least two, 2-h observation sessions per tracking period. However, heavy rain or fog prevented us from attaining 16 h of observation for five females. While following a female we recorded her position and behavior and those of her social mate at the start of each 5-min interval during the 2-h observation session; especially interesting behavior throughout the observation was recorded whenever it occurred. We quantified the behavior that we recorded at the beginning of each 5-min interval as a percentage of the total number of 5-min intervals.

We analyzed the following female behavior that we deemed relevant to our question about EPCs: location, foraging, and vocalizing (twitters, trills). Trills resemble male song, except that they are flatter. Twitters are high-pitched soft contact calls given by both sexes. Intrusions and copulations were recorded whenever they occurred.

We noted all female forays off their social mate's territory. We categorized these forays into long- and short-distance movements. Long-distance forays were movements across an immediately neighboring male's boundary and beyond his territory, followed by a return home. Short-distance forays were movements into

an adjacent territory. We also noted all observed intrusions onto the female's home range and the activities of all juncos present.

Male behavior during tracking

Behaviors recorded for males included song, visible display, foraging, perching above the female, and distance ($< 5\,$m or $> 5\,$m) from the female. Song consisted of two categories: long range song (LRS) which is used primarily in intrasexual interactions, and short range song (SRS) (Titus et al. 1997), used too rarely to include in our analyses. Visible display consisted of ptiloerection, erection of body feathers and fanning the tail to expose the white outer rectrices (Hill et al. 1999). For non-radio tagged males, if the female could be seen but the male could not, we assumed that he was $> 5\,$m from her. When the male was radio-tagged, determination of distance from the female was more precise; in that case our categories included $> 30\,$m.

Mapping Home Range

At 15-min intervals throughout the 2-h tracking sessions, we noted and marked female locations (fixes) with numbered flagging tape. To avoid artificially affecting a female's movements, we put flags in place only after the female had moved at least 10 m from the location. In 1998, we used a bicoordinate system to map female location fixes, in which we established transects through the home range and then measured distances to the transects using Sonin Combo Pro Electronic Distance Measurers; in some instances we simply measured distance to the transect with a 50-m open reel measuring tape or a Rolatape Distance Measuring Wheel. In 1999, we established fixes with a Trimble Global Positioning System with differential correction, accurate to $< 1\,$m.

From maps of female fixes we calculated the total area (home range) for the respective females, using HomeRange Version 2.1.4 (Huber and Bradbury 1999). We used the Minimum Convex Polygon method (Stickel, 1954) to produce a maximum estimate of home range. We also used the Fourier method (Anderson 1982), which estimates home range by focusing on the frequency of the individual's presence at each location (i.e. fix). With the Fourier method we calculated the areas that an individual occupied 95% of the time [Map (95)] and 50% of the time [Map (50)]. Map (50) was taken as a measure of the size of the 'core' home range. Chandler et al. (1994) applied the same methods in their study of male junco movements at MLBS, which permits us to compare our results with theirs.

Statistical Analyses

Non-parametric procedures were used as a result of non-homogeneity of variances and non-normal distribution of data. We used Mann–Whitney U-tests

to compare female home-range sizes and frequencies of behaviors of both sexes with regard to male treatment. When estimating power of the Mann–Whitney U-tests to detect significant differences, we employed relatively large effect sizes and based that decision on previous studies of the direct influence of testosterone on male home-range size (Chandler et al. 1994, 1997). During some stages of reproduction (when females are incubating or tending nestlings), treatment with testosterone increases male home-range size by 300–400% (Chandler et al. 1994). However, when females are fertile, testosterone and control males do not differ significantly in home-range size (Chandler et al. 1997). Previous comparisons of male juncos had high statistical power at an expected difference of 100% in male home ranges (Chandler et al. 1997). Thus, we estimated power to detect treatment-related differences in female home range of 50 and 100%, and for behavior we calculated power to detect effect sizes of 50%.

We used the PASS 2000 program (available from NCSS Statistical Software, Kaysville, UT, USA) to calculate the power of our Mann–Whitney tests. We assumed a normal distribution for these power calculations as this provided the most conservative estimates of power and because our data did not show significant skew or kurtosis. We represent our data either as ($\tilde{x}$) medians with interquartile ranges or as mean ($\bar{x}$) with standard errors. All tests are two-tailed unless otherwise indicated. Times are Eastern Daylight Time.

Results

Tracking Effort

Each female (n = 13) was tracked for an average of 3.8 ± 0.3 d (range: 2–6 d), and we accumulated an average of 15 h per female (range: 10–20.5). The number of fixes did not differ significantly (Mann–Whitney U = 17.5, p = 0.71) between T-mated females ($\tilde{x} = 72.0$, range: 50–89) and C-mated females ($\tilde{x} = 71.5$, range: 54–77).

Female home range

The $\tilde{x}$ minimum convex polygon-sized home range was 2.22 ha for all females combined (Table 1). The Map (95) home range estimate was 1.45 ha, and the Map (50) value was 0.43 ha. Home-range size did not differ significantly between T-mated and C-mated females for any of the three estimates (Table 1). The large range for the T-mated female minimum convex polygon can be attributed to one female that had a particularly large home range (17 ha), because she once made an hour-long foray that took her several hundred meters from her mate's territory. There was some overlap in female home ranges because neighbors sometimes foraged into territories defended by neighboring females' mates. Our tests were powerful enough to detect large differences in home-range size (50–100%) had they been there, but we did not find them.

Table 1: Median (interquartile range) home-range size of all females combined and of females mated to T- and C-males. Extreme values are given in parentheses below x̃

	n	Convex polygon (ha)	Map (95) (ha)	Map (50) (ha)
All females	13	2.22 (1.87)	1.45 (0.96)	0.43 (0.16)
C-mated females	8	2.17 (1.23)	1.53 (1.16)	0.45 (0.35)
		(1.47 – 4.29)	(0.67 – 3.00)	(0.23 – 0.96)
T-mated females	5	2.52 (5.15)	1.27 (0.53)	0.41 (0.06)
		(1.70 – 17.10)	(0.89 – 1.93)	(0.25 – 0.43)
P value[a]		0.77	0.28	0.15
Power (100%)[b]		0.18 (0.99)[c]	0.98	0.99
Power (50%)[b]		0.10 (0.61)[c]	0.58	0.61
C-males[d]	6	2.11 ± 0.22	0.38 ± 0.04	
T-males[d]	7	2.95 ± 0.45	0.55 ± 0.08	

[a] Results of one-tailed Mann–Whitney U-tests comparing C- and T-mated females.
[b] Power to detect a 100 and a 50% difference between the x̄ for each measure of home-range size assuming an approximate normal distribution.
[c] Numbers in parentheses exclude one outlier data point of 17.1.
[d] From Chandler et al. (1997). Values are given as x̄ ± SE.

Female forays

Short-distance forays were made by six (46%) of the females. The average duration of seven forays was 14.2 min (range: 5–30 min). In most cases the female either moved onto a neighboring territory and perched or foraged without interacting with other juncos. Three (60%) T-mated females and three (38%) C-mated females made short-distance forays.

Long-distance forays lasted from 30 min to 3 h and usually occurred in the early morning. We include in this category the forays of three additional C-mated females for which we were unable to map part of the home range. Long-distance forays occurred in six (38%) of 16 females. Typically they moved high in the canopy during long-distance forays, behaving covertly and pausing occasionally. Our definition of foray included only movements in which the female both left and returned to her mate's territory; we emphasize that half the females that made long-distance forays eventually deserted their mates. Male treatment was apparently not associated with the proportions of T-mated (n = 2, 40%) and C-mated (n = 4, 36%) females that made long-distance forays.

Female Behavior

Females of both treatment groups spent about half their time foraging (C-females: x̃ = 0.50; T-females: x̃ = 0.49) and there was no significant difference according to treatment (Mann–Whitney U, U = 17, p = 0.66; Power = 0.78). Trill vocalizations were uncommon and given primarily during intrusions by male neighbors or aggressive interactions with social mates. There was no detectable

effect of male treatment on number of female trills (Mann–Whitney U, U = 15, p = 0.23, one-tailed; Power = 0.08) (C-mated females: $\tilde{x}$ = 0.01; T-mated females: $\tilde{x}$ = 0.01). Twitter calls were given primarily during flight or while perched, never in the presence of intruders. Males usually made no apparent response to twitters. Female twitter calls did not vary significantly according to male treatment (Mann–Whitney U, U = 15, p = 0.23, one-tailed; Power = 0.11) (C-mated females: $\tilde{x}$ = 0.02; T-mated females: $\tilde{x}$ = 0.01). Power to detect a 50% difference in trills and twitters between C- and T-mated females was very low because these calls were given so infrequently.

Male Behavior

Control males spent significantly more time within 5 m of their mates than did T-males (Table 2). They also displayed more and spent more time perched above females, but these differences were not significant. T- and C-males spent similar amounts of time singing LRS. Considering only the six males wearing transmitters (which let us determine distance more accurately), T-males were somewhat more likely to be greater than 30 m from their mates than C-males (p = 0.06).

Discussion

Female Home Range

Little is known about the spatial activity of female songbirds during their fertile period. Because their movements can be furtive, radio-tracking is essential to follow them around, especially off their social mate's territory (Neudorf et al. 1997; Double and Cockburn 2000). We calculated three different estimates of the area of female activity. The minimum convex polygon included all points at which the female was found. Map (95) excludes the outer 5% of the fixes, and Map (50) excludes 50%. According to the hypothesis that female juncos obtain their EPC matings by moving off their social mate's territory, we

Table 2: Median (interquartile range) proportion of time that T-males (n = 5) and C-males (n = 8) engaged in various behaviors during their mate's fertile period

Behavior	T-male	C-male	P[a]
Forage	0.046 (0.069)	0.183 (0.113)	**0.005**
Perched above	0.056 (0.077)	0.106 (0.108)	0.143
Display	0.000 (0.007)	0.011 (0.036)	0.071
Long range song	0.130 (0.107)	0.130 (0.057)	0.88
Within 5 m of female	0.242 (0.278)	0.584 (0.244)	**0.028**
Greater than 30 m[b]	0.256 (0.119)	0.048 (0.128)	0.06

[a] Results of Mann–Whitney U-tests. Figures in bold are significant.
[b] Based on only the six pairs where males also had radio transmitters.

would expect their home ranges to be larger than, or similar in size to, home ranges of males. We found that female home-range size calculated as minimum convex polygons was about the same as that reported for males whose mates were fertile (Table 1; Chandler et al. 1997). Map (95) values of females in the present study were over three times larger than those reported for males by Chandler et al. (1997) suggesting that fertile females utilize space within the home range differently than do males. One possibility, having no relation to EPCs, is that males sing and watch ("guard") their social females especially during nest-building, spending most of their time on perches near the nest site, whereas females range more widely (as reported for certain other species; e.g. Nolan 1978; p. 146).

Home-range size did not differ significantly between T-mated and C-mated female juncos (Table 1). We used home-range size as an indicator of female propensity to foray into other territories for EPCs, predicting that females that foray more would have larger home ranges. However, female forays off territory were not related to male treatment. To our knowledge ours is the first study to calculate female home-range size with regard to EPC behavior. Only a few studies have radio-tracked females to examine incidence of forays (see Smiseth and Amundsen 1995; Neudorf et al. 1997; Double and Cockburn 2000). Each of these studies showed that fertile females often made multiple forays onto neighboring territories and in some cases traveled beyond adjacent neighboring territories. If C-mated female juncos regularly seek EPCs off their mates' territories, we would expect to see fairly large home ranges compared with those not seeking EPCs and thus not making forays. The statistical power of our tests was adequate for detecting large differences in home-range size (Table 1), but smaller differences may have gone undetected because of our small sample size and large variation in home-range sizes among females. Nevertheless, our results provide no support for the hypothesis that female juncos make large-scale adjustments in home-range size according to differences in attractiveness (i.e. testosterone levels) of their social mates.

Long-distance forays

Six of the radio-tracked females made long-distance forays. These lasted over 30 min and took the females through and beyond the territories of immediately adjoining neighboring males. The birds moved covertly and stayed high in the canopy, and we observed no copulations or social interactions during the forays (although the females often moved too quickly to be kept in sight continuously). Long-distance forays appeared not to be associated with male treatment, and five of the six were made after nest failure and before renesting; one female made a foray during nest building. Interestingly, three of the six females that made these forays eventually deserted their mates within 2–3 d of initiating their forays, when they probably had time to join a different male and renest. Thus a possible function of long-distance forays is that they permit the female to compare her social mate with other potential mates. Mate switching has been reported in

juncos although it is rare (3% within a single season and 10–20% between years; Ketterson et al. 1992). Hovi and Rätti (1994) showed that female pied flycatchers (*Ficedula hypolecua*) visit several males during initial mate choice, often doing so covertly. Mate switching in other species often follows unsuccessful nesting attempts with the first social mate. In several species, between-season mate switching by females has been attributed to the failure of previous nesting attempts (e.g. Johnston and Ryder 1987; Lindén 1991; Choudhury 1995).

The disturbance of being caught for radio-tagging, or the combination of radio-tagging and being subjected to our "nest predation" (three females) could have had an effect on female desertion of the social male. However, juncos are very tolerant of handling and of close observation by humans. Thus, we conclude that the forays we observed were probably a normal aspect of female junco breeding behavior and not an artifact of our study. Clearly, the function of long-distance forays requires further investigation.

Do female juncos engage in EPC-inducing tactics?

Extra-territorial forays by female juncos were less frequent than those reported for certain other female passerines, in which 80% of females made forays (e.g. Smiseth and Amundsen 1995; Neudorf et al. 1997). During short-distance forays female juncos usually foraged and did not associate with neighboring juncos. Fertile female bluethroats (*Luscinia s. svecica*) frequently made extra-territorial forays and often foraged during these forays; Smiseth and Amundsen (1995) suggested that they were simultaneously assessing resource availability and the eligibility of potential extra-pair mates. We cannot rule out this possibility for female juncos; but if extra-pair mate assessment is the primary function of forays and if males with high levels of testosterone are more attractive in nature, we would expect forays by C-mated females to be more frequent than in T-mated females. We found no such difference.

Intrusions by neighboring males and unidentified males occurred frequently during almost 200 h of continuous tracking, and these gave females many opportunities to participate in EPCs. However, we observed none. We did see within-pair copulations, but rarely, and these showed no pattern of distribution during the day (Neudorf, Ketterson and Nolan, unpubl. data). The absence of pattern is consistent with findings from other studies (Smith 1988; Venier et al. 1993; Hanski 1994; but see Westneat 1993), in which both extra-pair and within-pair copulations occured throughout the day. Interestingly, Double and Cockburn (2000) found that female superb fairy-wrens (*Malurus cyaneus*) made forays off territory and obtained EPCs with neighboring males during pre-dawn hours. In a separate study we tracked female juncos as they left their roosts in the morning, but we observed no behavior that we could associate with EPCs. In fact, during the fertile period social pairs often roosted together, and sometimes both sexes roosted together outside their home territory (Ziolkowski, Neudorf, Ketterson and Nolan, unpubl. data). The fact that we saw within-pair copulations

but not EPCs suggests that EPCs are rarer, or possibly less conspicuous, than within-pair copulations in juncos.

We observed one female junco refuse a copulation by her mate indicating that females have some control over the occurrence of copulations. In certain other species females are known to exert choice of extra-pair mates through refusal or acceptance of attempts to copulate by males that intrude on their home ranges (e.g. Møller 1988; Dickinson 1997).

Previous studies have shown that fewer T-male juncos than C-males lose paternity of young produced by their social mates (Raouf et al. 1997). Apparently, this is not the result of closer mate-guarding by T-males. Chandler et al. (1997) observed no significant difference between the average distance separating T-males and C-males from their mates, and we found that T-males spent less time than C-males within 5 m of their females. This contrasts with findings of Saino and Møller (1995) who reported that male barn swallows (*Hirundo rustica*) treated with testosterone spent more time than controls near their mates. T-male juncos also engaged in fewer displays, possibly because they were more distant from their mates. Together the EPF findings of Raouf et al. (1997) and our behavioral data suggest that although free-living T-males are less attentive, they are still preferred by females.

Females showed no indication that they advertise their fertility. We observed instead that they often flew away from fights between the social male and an intruding male, and that they frequently gave aggressive trills and occasionally alarm calls during these interactions. Female calls could incite males to compete by alerting the social mate to the presence of the intruder, although the number of female trills did not differ between T- and C-mated individuals. The power of our tests was low because of the infrequent use of these vocalizations by females. The observation that trills and twitters were given infrequently suggests that these vocalizations are not likely used in fertility advertisement.

In summary, fertile female juncos sometimes made forays from the territories of their social mates and occasionally eventually deserted them. However, we found no detectable relationship between female behavior and male treatment; and if extra-territorial forays are a tactic for obtaining EPCs, the propensity to do so appears not to be associated with male testosterone treatment. Males frequently intrude on the home range of fertile females, which would create EPC opportunities, but we observed none. Although studies of mate choice by captive females have shown that they prefer T-males (Enstrom et al. 1997), we could find no detectable behavioral evidence for the existence of a preference in this study of juncos in nature.

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