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Original Article

Failed despots and the equitable distribution of fitness in a subsidized species

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Territorial species are often predicted to adhere to an ideal despotic distribution and under-match local food resources, meaning that individuals in high-quality habitat achieve higher fitness than those in low-quality habitat. However, conditions such as high density, territory compression, and frequent territorial disputes in high-quality habitat are expected to cause habitat quality to decline as population density increases and, instead, promote resource matching. We studied a highly human-subsidized and under-matched population of Steller's jays (*Cyanocitta stelleri*) to determine how under-matching is maintained despite high densities, compressed territories, and frequent agonistic behaviors, which should promote resource matching. We examined the distribution of fitness among individuals in high-quality, subsidized habitat, by categorizing jays into dominance classes and characterizing individual consumption of human food, body condition, fecundity, and core area size and spatial distribution. Individuals of all dominance classes consumed similar amounts of human food and had similar body condition and fecundity. However, the most dominant individuals maintained smaller core areas that had greater overlap with subsidized habitat than those of subordinates. Thus, we found that (1) jays attain high densities in subsidized areas because dominant individuals do not exclude subordinates from human food subsidies and (2) jay densities do not reach the level necessary to facilitate resource matching because dominant individuals monopolize space in subsidized areas. Our results suggest that human-modified landscapes may decouple dominance from fitness and that incomplete exclusion of subordinates may be a common mechanism underpinning high densities and creating source populations of synanthropic species in subsidized environments.

Key words: ***Cyanocitta stelleri*, density dependence, fitness, habitat selection, human food subsidy, ideal despotic distribution, resource under-matching, Steller's jay.**

INTRODUCTION

Ecological theory predicts that the distribution of individuals in landscapes with heterogeneously distributed food resources is a function of habitat selection strategies, mediated by social system (Fretwell and Lucas 1969). For territorial species, habitat selection is often influenced by unequal competitive abilities, and organisms are predicted to adhere to an ideal despotic distribution (Fretwell 1972; Calsbeek and Sinervo 2002). Under an ideal despotic distribution, dominant ("despotic") individuals exclude subordinates from high-quality habitat containing relatively abundant food resources, compelling them to instead use lower-quality habitat with fewer food resources. In these situations, territorial exclusion is predicted to result in the under-exploitation of food resources in high-quality habitat (i.e., resource under-matching) such that individual fitness is greater in high- than in low-quality habitat (Fretwell 1972; Kennedy and Gray 1993). Under this scenario, the most dominant individuals are predicted to secure the highest quality territories and gain a fitness benefit from doing so (Carpenter and MacMillen 1976; Gill and Wolf 1977; Calsbeek and Sinervo 2002).

The predictions of the ideal despotic distribution and resource under-matching have held for some territorial species (Andren 1990; Lin and Batzli 2001; Calsbeek and Sinervo 2002), but certain conditions can lead to the breakdown of the ideal despotic distribution and instead promote resource matching. Territoriality, a prerequisite of the ideal despotic distribution, can break down when food resources are abundant and the cost of defending them outweighs the benefit gained by excluding subordinates (Carpenter and MacMillen 1976; Hixon 1980). Additionally, high densities of competitors can lead to territory compression (or "shrinkage") and to more frequent territorial disputes, which can reduce individual fitness in purportedly high-quality habitat (i.e., under-matching; Pusenius and Schmidt 2002; Ridley et al. 2004; Haché et al. 2013). Both of these processes could lead to departures from the expectations of the ideal despotic distribution and instead

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promote resource matching, where habitat quality declines as population density increases until fitness becomes equivalent between high- and low-quality habitats (Pulliam and Caraco 1984; Fagen 1987; Tregenza 1995). Thus, the defensibility of resources plays a key role in determining the extent to which social systems, and specifically territoriality, shape the distribution and fitness of individuals. While the classic concept of the ideal despotic distribution may sometimes be unrealistic for natural populations (Kennedy and Gray 1993), it provides a useful starting point for testing ideas about how the distribution of resources facilitates habitat selection strategies and the distribution of organisms, especially in human-modified systems.

Human food subsidies are one example of an often abundant and stable resource that may be difficult to defend and could affect habitat selection and the distribution of fitness. Human food subsidies are a global phenomenon with myriad ecological and evolutionary consequences for biodiversity (Oro et al. 2013; Newsome et al. 2015). Landscapes that are highly influenced by human activity are often an abundant source of such subsidies (Marzluff and Neatherlin 2006; Oro et al. 2013), which can alter territorial behavior (Evans et al. 2010; Scales et al. 2011; Hardman and Dalesman 2018), social systems (McGowan 2001; Václav et al. 2003; Robb et al. 2008), and space use (O'Donnell and DelBarco-Trillo 2020). Human food subsidies also commonly promote high densities of synanthropic species (Marzluff et al. 2001; Prange et al. 2003; Shochat 2004). In some cases, subsidies can improve the fitness of species (Tortosa et al. 2002; Olea and Baglione 2008), but landscapes with human food subsidies can also function as "ecological traps" where abundant human "junk food" holds little nutritional value and is, thus, a poor indicator of habitat quality (Gates and Gysel 1978; Schlaepfer et al. 2002). In this situation, areas with abundant food subsidies and high population densities could result in increased competition and subsequently low individual fitness (Marzluff et al. 2001; Shochat 2004). Because synanthropes often utilize human food subsidies, they can provide valuable opportunities for understanding how human subsidies affect habitat selection and social systems and, ultimately, influence individual and population-level fitness.

Here, we studied a population of Steller's jays (*Cyanocitta stelleri*), a common territorial and synanthropic bird species in the forests of western North America, that are under-matched to abundant human food resources in subsidized habitats (i.e., campgrounds). In this system, average body condition and fecundity are higher in subsidized campground areas than unsubsidized habitats away from campgrounds (West and Peery 2017). Subsidies also promote high survival of both adults and juveniles such that campgrounds act as a population source for jays (West et al. 2019). However, resource under-matching in this system is contrary to expectations, as exceptionally high population density, compressed and overlapping territories, and frequent agonistic interactions between jays (West and Peery 2017) should theoretically reduce the benefit of settling in resource-rich environments and facilitate similar fitness outcomes between subsidized and unsubsidized habitats (Ridley et al. 2004; Shochat et al. 2006). Additionally, Steller's jays typically exhibit incomplete territoriality, in which individuals are most dominant at the center of their territory and less dominant towards the periphery (Brown 1963), and this social system may promote departures from the expectations of the ideal despotic distribution and resource under-matching.

To understand how resource under-matching persists in this system, we assessed how individual subsidy consumption, fitness, and space use varied as a function of social dominance within high-quality, subsidized habitat. Because previous studies demonstrated that areas with abundant human food subsidies constitute high-quality habitat for Steller's jays rather than an ecological trap (West and Peery 2017; West et al. 2019), we posited two alternative hypotheses for how under-matching could be maintained, while population-level fitness remained high. Under the "many losers" hypothesis, we predicted that socially dominant individuals were sufficiently effective at monopolizing food resources such that they, individually, achieved such high fecundities that population-level reproductive rates were high in subsidized habitats. Under this hypothesis, we predicted that socially dominant individuals would eat more human foods, achieve elevated body condition and fecundity, and hold smaller territories than subordinate individuals. Alternatively, under the "many winners" hypothesis, we predicted that dominant individuals would not be effective at excluding subordinates from food resources and that observed high population-level reproductive rates were the result of high individual fecundities that were similar across social classes. Under this hypothesis, we predicted similar human food consumption, fitness, and space use among dominance classes. Testing these hypotheses helps to elucidate mechanisms promoting the commonly observed phenomenon of high densities of synanthropic species in human-dominated, subsidized landscapes. Furthermore, as the impacts of human food subsidies are unlikely to diminish in the future, understanding how habitat selection strategies and social systems are modified under their influence is important for conservation and predicting wildlife distributions.

MATERIALS AND METHODS

Study system and sampling

We studied populations of Steller's jays in two campgrounds within Big Basin Redwoods State Park, Santa Cruz County, California (hereafter Big Basin; Figure 1), to test our hypotheses about resource under-matching. Because of the availability of human food subsidies and previously established high fitness of jays utilizing campground areas, we considered campgrounds to be high-quality habitat and surrounding forest areas to be of lower quality (West and Peery 2017; West et al. 2019). We collected data during three breeding seasons, mid-May—mid-August, in 2017, 2018, and 2019. We captured and banded jays with unique color combinations for individual recognition and to assess individual fitness (see next sections). We used call playback and a combination of mist nets (Avinet Research Supply) and live traps (Havahart and homemade) to capture jays during all 3 years of the study. To characterize jay space use, we also deployed radio transmitters (Model A1070, Advanced Telemetry Systems) on jays using backpack-style harnesses made of 0.1″ natural tubular spectra tape (Bally Ribbon Mills) in each year of the study. Handling time was kept to a minimum (usually <5 min, slightly longer for birds receiving radio tags), and samples taken are discussed in the subsequent sections. All appropriate guidelines for humane and ethical use of animals in research were followed, and research was conducted under IACUC protocol A005411-R01-A01 and scientific collection permit SC-13714. To the best of our knowledge, no Steller's jays were injured or died as a result of our activities.

To examine jay space use, we tracked each radio-tagged jay to determine their precise location (± 10 m) 25–35 times per season. We allowed at least 2 h between relocations of the same individual to ensure independence between relocations (Swihart and Slade

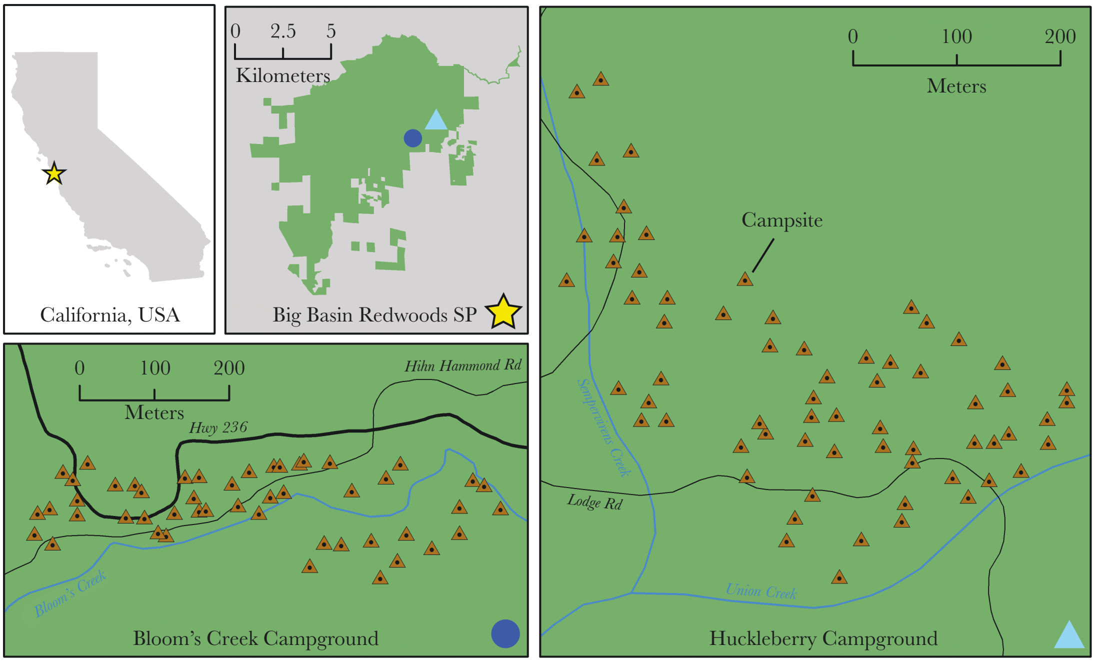

Figure 1
Map of the study area.

1985), and we varied the time of day during which we tracked individuals. We also collected roost locations (between 2200 and 0300) to ensure that we fully characterized jay home ranges. We tracked birds by searching on foot with telemetry equipment and marked jay locations using a handheld GPS unit. Observations of jays and jay behavior throughout the breeding season allowed us to assess the breeding status of jays and determine the identities of socially monogamous jay pairs. We only used male jays for these analyses because female jays are generally subordinate to males (Brown 1963), and our sample size of uniquely identified females did not allow dominance assessment.

Defining dominance classes

We classified jays into dominance classes by conducting controlled feeding trials (hereafter "behavior trials") at picnic tables. Because jays have site-based dominance where territorial defense typically weakens as distance from the nest site increases (Brown 1963), we determined a dominance ranking of jays at individual picnic tables dispersed throughout the entire campground to ensure we fully captured spatial variation in dominance for each individual. During each trial, we placed approximately 10 peanuts at the center of a picnic table and then observed jays as they interacted with conspecifics to exploit the food source (Brown 1963; West and Peery 2017). We recorded every banded individual present at each trial, the winner and loser of each interaction, and the aggression level of each interaction on a 0–5 scale. An aggression level of zero indicated that individuals did not interact when feeding at the same time on a table, and so no winner was recorded. Aggression levels were defined as follows: 1: one jay wing-flapped and vocalized with an "aap" or "wek" call at another; 2: one jay displaced another; 3: one jay chased another; 4: jays aggressively sidled with one another but did not make contact; 5: jays physically fought with one another (West and Peery 2017). We evaluated the results of behavior trials to determine the most dominant bird at each table. To be considered dominant at a table, an individual had to win at least three interactions at that table. At each table, an individual was considered dominant if it won the most interactions at that table or if it always won interactions against the bird that won the most interactions. In cases where there was not a consistent winner between two individuals that consistently won against all other individuals, or where consistent winners did not interact with one another, we classified the bird with the higher average aggression score in contests that they won as dominant. In cases where individuals' wins and aggression scores tied, both were considered dominant at a given table. An individual was also considered dominant at a given table if it was the only individual (with the exception of its mate) to appear for two or more 15-min trials at a specific table on different days. There were occasionally tables at which not enough interactions occurred to determine a dominant bird. We conducted between one and six trials at each of 49 picnic tables in Bloom's Creek Campground and 65 picnic tables in Huckleberry Campground each year.

We determined dominance for each year separately because dominance and core areas could shift from year to year. Within each year, we overlaid core areas (see below for core area delineation methods) in ArcMap (version 10.7; ESRI 2019) with the results of the behavior trials at each picnic table, and then classified jays into three social classes. "High" dominance included individuals that were dominant at tables within and outside their core area, "medium" dominance included individuals that were dominant only within their core area, and "low" dominance included individuals that were not dominant anywhere within the campground (Figure 2). We used this method, rather than traditional Elo-ratings or other established methods because jay dominance hierarchies shift spatially throughout a given area (Brown 1963) and because we were simply interested in identifying the most dominant individual rather than revealing the entire dominance hierarchy.

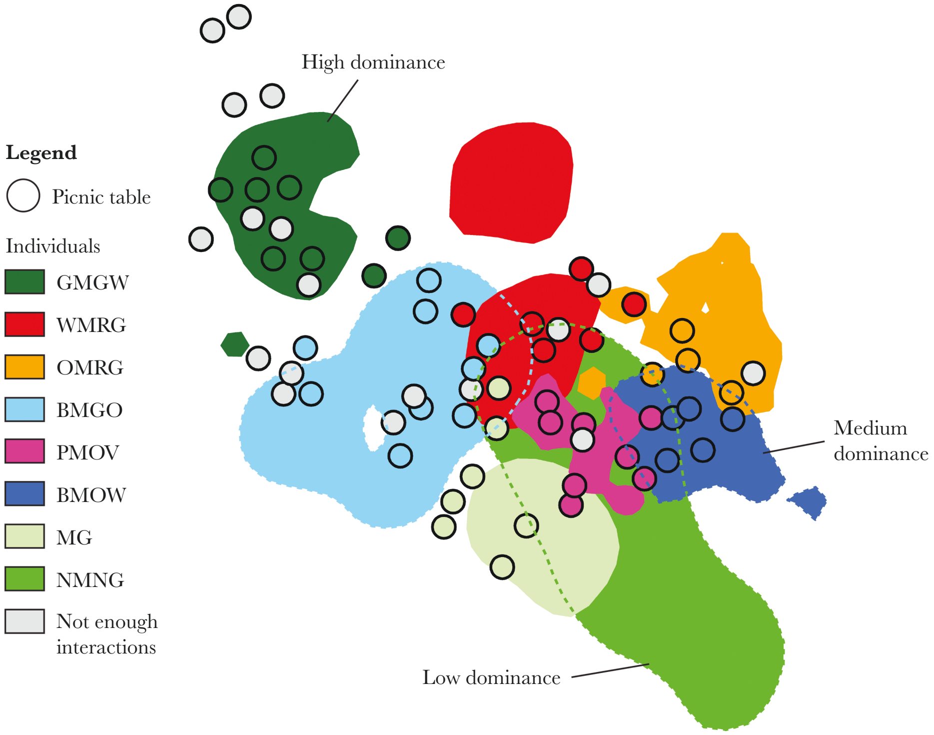

Figure 2
Core areas of individual jays overlaid with picnic tables in Huckleberry Campground in 2019. Picnic table color matches the color of the core area of the bird that was dominant at the table. One example each of a high, medium, and low dominance bird are labeled. Gray tables represent sites where we did not record enough interactions to determine dominance.

Human food subsidy consumption

We evaluated individual consumption of human food subsidies using stable isotope analysis of $\delta^{13}C$ in primary feathers. $\delta^{13}C$ is a useful indicator of human food consumption because human foods are often made up of corn (a C_4 plant) and corn byproducts, making them enriched in the heavy isotope of carbon. This makes them isotopically distinguishable from natural prey items in western North America because primary production in this area is driven by native C_3 plants (Newsome et al. 2010; West et al. 2016). We clipped approximately 50 mm of the most recently grown new primary flight feather from each captured jay at the end of the breeding season (early-mid August) at least 40 days after the conclusion of behavior trials. Because feathers incorporate the isotopic signature of the diet during periods of feather growth (Hobson and Clark 1992) and a primary feather takes approximately 30 days to grow, these feather samples represented breeding season diet but were not contaminated by any peanut consumption that occurred during the behavior trials. We rinsed feather samples thrice in 2:1 chloroform:methanol solution to remove surface contaminants and then homogenized them using scissors. Homogenized feathers were dried for approximately 72 h at 55 °C. Analysis of $\delta^{13}C$ was conducted at the University of New Mexico Center for Stable Isotopes using a Thermo Scientific Delta V mass spectrometer connected to a high-temperature conversion elemental analyzer and a Costech 4010 elemental analyzer. We report $\delta^{13}C$ results as parts per mil (‰) ratio relative to the international standard, Vienna-Pee Dee Belemnite limestone. We examined the relationship between dominance class and human food subsidy consumption using a linear mixed model with individual as a random effect because we captured some of the same individuals in multiple years of the study. We used $\delta^{13}C$ as the continuous response variable and categorical dominance class (i.e., low, medium, high) as the fixed effect. We also included year as a fixed effect to correct for some heteroscedasticity in the residuals. Results are presented as the estimated marginal mean averaged over the 3 years of the study and a 95% confidence interval.

Fitness metrics

To understand how fitness was distributed among birds in different dominance classes, we collected data on body condition (i.e., body mass and growth bar width) and annual fecundity (i.e., number of fledged young). We conducted analyses using the “lme4” package (version 1.1-21; Bates et al. 2015) and compared means between dominance classes when necessary using the “emmeans” package (version 1.6.1; Lenth 2021) in the R Statistical Environment (R Core Team 2020).

We measured two indices of body condition: body mass and growth bar width. We measured body mass using a Pesola scale when birds were recaptured at the end of the breeding season (early-mid August). We standardized body mass for body size using tarsus length cubed, an index of body volume (West and Peery 2017). We measured tarsus length using calipers during the same capture event at which body mass was measured. We then multiplied these values by 10 000 for ease in reporting results. We first evaluated body mass among the dominance classes using a linear mixed model with individual as a random effect. However, the variance of the random effect was estimated as zero, and thus we removed it and simply used a two-way ANOVA. Standardized body mass was the continuous response variable, and we used dominance class and year as categorical factors. We did not include an interaction effect between dominance class and year because there was no reason to expect a different relationship between body mass and dominance among years.

We used growth bar width as another indicator of individual body condition. A feather growth bar consists of one dark band produced during the day, and one light band, produced at night (Wood 1950). Together, one set of bands constitutes feather growth in a 24-h period (Wood 1950; Grubb 2006). Feather growth is energetically costly, and therefore the ability to grow feathers faster (i.e., wider growth bars) is positively correlated with nutritional status (Grubb 1991). We collected the newest newly grown rectrix, determined by molt pattern and presence of feather sheaths, from each jay recaptured at the end of the breeding season, at least 40 d after the conclusion of behavior trials. Growth bars reflect nutrition during the time of feather growth and thus, because we took a newly grown feather, growth bar width was not contaminated by any peanuts that may have been consumed during the behavior trials. We standardized growth bar width by body size using tarsus length cubed, as we did for body mass, and multiplied it by 100 000 for ease in reporting. We then used a linear mixed model with individual as a random effect to assess the relationship between dominance class and growth bar width. We used standardized growth bar width as the continuous response variable and we used dominance class and year as additive fixed effects. Results are presented as the estimated marginal mean averaged over the 3 years of the study and a 95% confidence interval.

We estimated annual fecundity (i.e., number of fledglings produced) for individual jays by either locating and monitoring nests until the young fledged ($n = 4$) or by following radio-tagged birds and observing how many fledglings they interacted with (e.g. begging or feeding behavior; $n = 47$). Fledgling Steller's jays follow and receive food from their parents for 30 d or more after fledging (Walker et al. 2020; EHW and KB, personal communication), so it was possible to determine nest success and number of fledglings by closely observing both members of the pair after nesting was completed. When possible, we also banded juveniles so that we could discern identities when we observed family groups on multiple occasions. While locating nests and measuring components of reproduction like lay date, clutch size, hatching success, and nestling condition would have been ideal, we did not have the resources to conduct thorough nest searches. We instead used fledging success as our measure of annual fecundity (Weatherhead and Dufour 2000).

We treated annual fecundity in two different ways for analysis. We first considered annual fecundity as continuous and compared the mean number of fledglings per male per year among dominance classes using a linear mixed model with individual as a random effect. The variance of the random effect was estimated to be zero, so we removed it from the model and assumed independence among all annual fecundity estimates. Due to small sample sizes and non-normality in the distribution of fecundity data, we used a Kruskal–Wallis test for the final comparison of mean annual fecundity between dominance classes. In our second approach, we treated fecundity as a binary indicator of nest success by grouping birds according to whether they successfully fledged offspring or not. We then conducted a chi-squared test to determine if there was any relationship between ordinal dominance class and nest success.

Space use

To characterize jay space use, we delineated home ranges and core areas for each radio-tagged individual. We defined a home range as the 95% utilization distribution for each individual jay (West et al. 2016), and we analyzed relocation data using the adehabitatHR package (Calenge 2006) in the R Statistical Environment (R Core Team 2020). Next, we delineated core areas following methods from Vander Wal and Rodgers (2012). Specifically, we plotted each jay's utilization distribution area against the isopleth volume (Supplementary Figure S1) and identified the isopleth at which the slope was closest to one (Vander Wal and Rodgers 2012). This point represents the threshold at which proportional home range area begins to increase at a greater rate than the probability of use, and we used that isopleth to define the borders of each jay's core area (Vander Wal and Rodgers 2012). We chose this method, rather than using an arbitrary 50% utilization distribution, in an effort to ensure that our core areas accurately represented the areas that received the greatest use (see Supplementary Appendix S1 for a comparison of methods). Finally, we removed seven individuals from all further analyses because their core areas did not overlap campground areas, so we could not accurately assess their dominance class.

We originally planned to examine both core area size and home range size in relation to dominance class, but because these two measurements were highly positively correlated ($r = 0.97$), we only considered core area size. We log-transformed core area size to meet the assumption of normal distribution and then used a linear mixed model with individual as a random effect to examine the relationship between dominance class and core area size. The variance of the random effect was estimated as zero, so we removed it from the model and used a two-way ANOVA with dominance class and year as categorical factors. Results are presented as the estimated marginal mean averaged over the 3 years of the study and a 95% confidence interval.

To compare the spatial distribution of core areas in relation to high-quality habitat, we calculated the proportion of overlap between each individual's core area and the campground area. To delineate the campground boundary, we created a 10-m buffer around each campsite and used the minimum bounding geometry tool in ArcMap (version 10.7.1; ESRI 2019) to create minimum convex hull polygons around the two campgrounds. We calculated the area of overlap between individual core areas and campgrounds and then divided by the total area of individual core areas to determine the proportion of each individual's core area that overlapped with the campground. Steller's jays in their first breeding season rarely breed (Brown 1963, West and Peery 2017), and we observed that some of these individuals utilized a strategy of being subordinate "floaters" in which they maintained a high degree of overlap with campground areas. Our hypotheses were restricted to territorial, breeding jays, and we therefore included only individuals known to be in at least their second breeding season in this analysis. To test whether highly dominant individuals had more overlap with campgrounds than subordinates, we conducted a two-way ANOVA, with the proportion of core area overlap with campgrounds as the response, and dominance class and year as explanatory variables.

RESULTS

Defining dominance classes

Across the 3 years of the study, we classified 17 males as low dominance, 15 males as medium dominance, and 21 males as high dominance. In 2017, we conducted 152 behavior trials and recorded a total of 1057 dyadic interactions (83% with aggression score >0); in 2018, we conducted 151 behavior trials and recorded 1544 dyadic interactions (81% with aggression score >0); and in 2019, we conducted 183 behavior trials and recorded 1509 dyadic interactions (87% with aggression score >0). On average, low dominance males won 15% of all interactions (aggression score >0) in which they were involved, medium dominance males won 59%, and high dominance males won 75%. When high dominance males lost interactions, it was most often to other high dominance males (72% of losses). Indeed, considering only tables at which they were dominant, the dominant individual won 96% of the interactions in which they were involved, on average.

Human food subsidy consumption

We measured the human subsidy consumption of 45 individuals (n = 16 low dominance, n = 12 medium dominance, and n = 17 high dominance). Jays with low dominance (δ^{13}C = −21.2 ± 0.22‰), medium dominance (−21.2 ± 0.25‰), and high dominance (–21.0 ± 0.21‰) all had similar levels of subsidy consumption (δ^{13}C; P value for all pairwise comparisons >0.83; Figure 3A). There was no evidence of any difference in subsidy consumption among years (P value for all comparisons >0.50).

Fitness metrics

We measured body mass of 35 individuals (n = 14 low dominance, n = 8 medium dominance, and n = 13 high dominance). Body mass ranged from 110 to 127 g, while tarsus length ranged from 40.2 to 46.5 mm. Standardized body mass ranged from 11.5 to 18.6. Estimated marginal mean body mass for each dominance class was very similar (low: 15.0 ± 0.36, medium: 15.0 ± 0.47, high: 14.9 ± 0.37), and thus we found no evidence for a difference in body mass between dominance classes (P value for all comparisons >0.98). However, average body mass was higher in 2018 (estimated marginal mean = 16.0 ± 0.37) than in 2017 (14.4 ± 0.39; t_{30} = 3.04, P = 0.01) and 2019 (14.5 ± 0.43; t_{30} = 2.73, P = 0.03; Figure 3B).

We measured the average feather growth bar width of 42 individuals (n = 14 low dominance, n = 10 medium dominance, and n = 18 high dominance). Average growth bar width ranged from 2.1 to 5.3 mm, and standardized growth bar width ranged from 3.90 to 7.55. Estimated marginal mean growth bar width was similar for each dominance class (low: 5.14 ± 0.28, medium: 5.67 ± 0.32, high: 5.29 ± 0.25), and we found no evidence of differences between any groups (P value for all comparisons >0.39; Figure 3C). We also found no evidence for differences among years (P value for all comparisons >0.17).

We determined annual fecundity for 47 jays (n = 16 low dominance, n = 13 medium dominance, n = 18 high dominance) across the 3 years of the study. Fecundity estimates ranged from 0 to 4 fledglings, with 4 fledglings observed only once. Average annual fecundity estimates were quite similar for low (1.31, SE = 0.31), medium (1.15, SE = 0.34), and high (1.44, SE = 0.30) dominance individuals. Our Kruskal–Wallis test confirmed that there were no differences in average number of fledglings among dominance classes (H(2) = 0.37, P value = 0.83) (Figure 4A), and chi-squared tests also confirmed that distributions were independent even when fecundity data were considered as binary (i.e., success/failure; chi-squared = 0.63, df = 2, P value = 0.73).

Space use

We delineated core areas for 53 individuals (n = 17 low dominance, n = 15 medium dominance, n = 21 high dominance). Core areas had a high amount of overlap (Figure 2) and core area size varied considerably (range: 0.63–7.19 ha). Back-transformed estimated marginal mean core area sizes were similar for low (2.82 ± 1.14 ha) and medium (2.57 ± 1.13 ha; t_{48} = 0.53, P value = 0.86) dominance classes, but there was strong evidence that high-dominance individuals maintained smaller core areas (1.49 ± 1.11 ha) than low (t_{48} = 3.77, P value < 0.01) and medium (t_{48} = 3.18, P value < 0.01) dominance individuals (Figure 4B). We also found moderate evidence that core areas were larger in 2019 than in 2018 (t_{48} = –2.28, P value = 0.06), but there was no evidence of a difference between 2017 and 2018 (t_{48} = 1.00, P value = 0.58) or between 2017 and 2019 (t_{48} = –1.39, P value = 0.35).

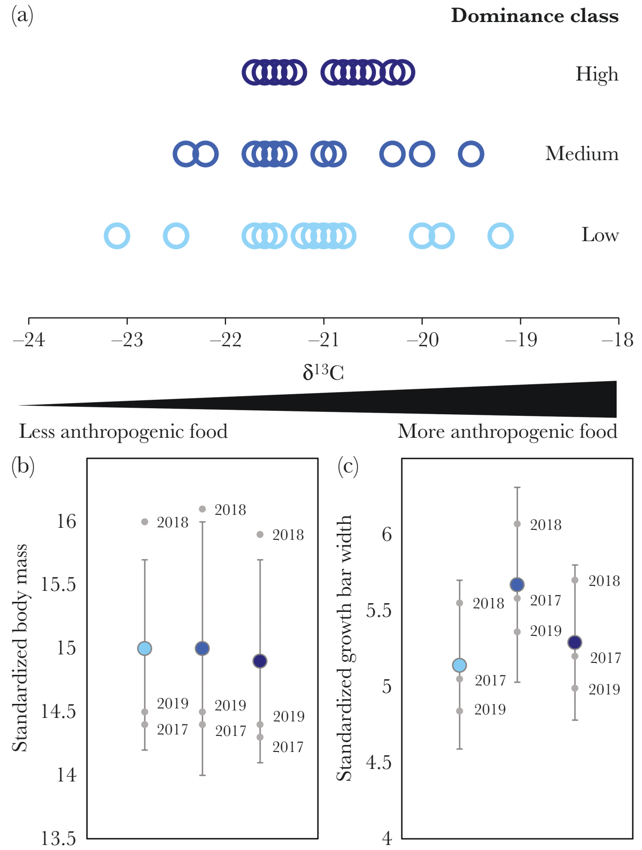

Figure 3

(A) The amount of anthropogenic food subsidies in the diet of individual jays in each dominance class, as measured by δ13C concentrations in feathers. Each circle represents one individual. (B) Estimated marginal mean body mass and 95% confidence interval for jays in each dominance class. Colored dot represents the mean over all years, and the estimated marginal means for each year of the study are shown in gray. (C) Estimated marginal mean growth bar width and 95% confidence interval for jays in each dominance class. Colored dot represents the mean over all years, and the estimated marginal means for each year of the study are shown in gray.

During our study, only a small number of birds in their first breeding season regularly used campgrounds (n = 5); however, these were all low dominance and had high average overlap between their core areas and campgrounds (0.78 ± 0.15). We never observed any of these “floaters” with a mate or participating in breeding or nesting behaviors, so we present results only for individuals known to be in at least their second breeding season. We assessed the spatial distribution of core areas for 39 territorial breeding individuals (n = 8 low dominance, n = 12 medium dominance, n = 19 high

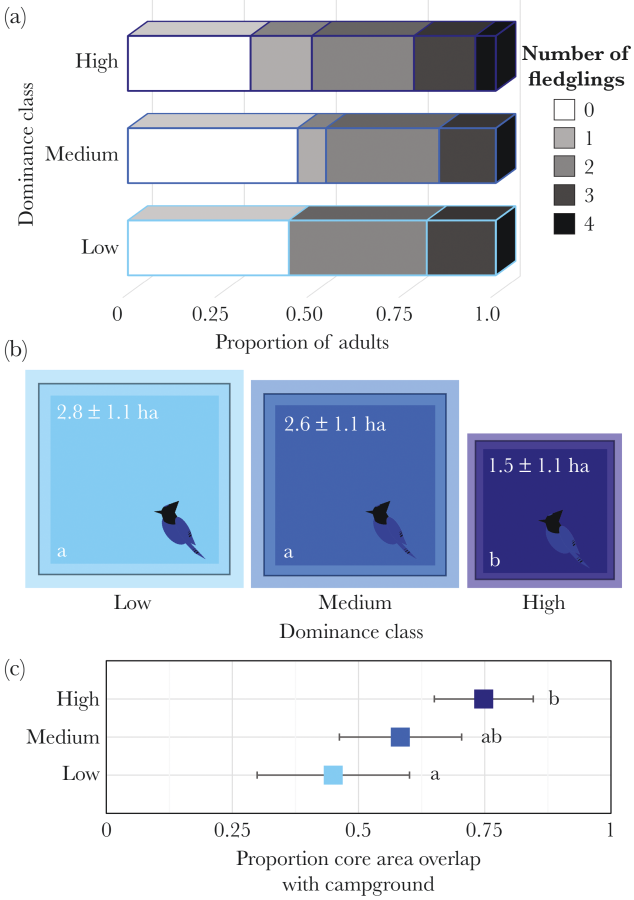

Figure 4

(A) Number of offspring fledged by adults in each dominance class over all years of the study. (B) Estimated marginal mean core area sizes for jays in each dominance class, averaged over the 3 years of the study (to scale). Inner- and outer-most squares represent 95% confidence intervals around the mean (gray line). (C) Mean proportion of core areas that overlapped with campgrounds for each dominance class. Error bars represent 95% confidence intervals. Letters denote significance.

dominance). There was strong evidence of a difference in mean overlap of core areas with the campground among all dominance classes ($F_{2,34} = 5.90$, P value < 0.01). Specifically, the core areas of high-dominance individuals (0.75 ± 0.05) overlapped campgrounds more than low (0.45 ± 0.07) dominance individuals ($t_{34} = 3.31$, $P < 0.01$). There was also weak evidence for a difference in overlap between high and medium (0.58 ± 0.06) dominance classes ($t_{34} = 2.17$, P value $= 0.09$), but there was no evidence of a difference between low and medium dominance classes ($t_{34} = 1.39$, P value $= 0.36$; Figure 4C). Thus, among territorial breeders, dominant individuals had more core area overlap with campgrounds on average than subordinate individuals (Supplementary Figure S2).

DISCUSSION

Our results suggest that, first, jays attain high densities in campgrounds because dominant jays do not exclude subordinates from human food subsidies. This conclusion is supported not only by stable isotope analyses, but also by observations both during and outside behavior trials, when we frequently observed subordinate jays accessing subsidies while dominant jays were chasing other individuals, caching food resources, or not present. Generally, competitor densities are expected to increase when food resources are dispersed (Goldberg et al. 2001), and increased densities can lead to reduced aggression because the cost of aggression outweighs the benefit of resource defense (Brown 1964; Goldberg et al. 2001). Consequently, we conclude that human food resources are too abundant and dispersed and dominant jays face too many competitors to be effective despots of abundant human subsidies.

Second, our results suggest that jay densities do not reach the level necessary to facilitate resource matching because dominant individuals monopolize space in subsidized campground areas. Highly dominant individuals maintained small core areas that overlapped significantly with subsidized campground areas. These areas likely provided the most reliable access to human subsidies and, thus, are perceived by jays as the highest quality for breeding. This observation is in line with the concept of economic defensibility (Brown 1964; Calsbeek and Sinervo 2002), which proposes that high territory quality is associated with small territory size because resources are highly concentrated and because territory defense is energetically costly (Carpenter and MacMillen 1976; Carpenter 1987). Under an ideal despotic distribution, subordinate individuals are predicted to use more space to meet their nutritional needs (Calsbeek and Sinervo 2002; Sells and Mitchell 2020), which we also observed in our study area. Subordinate individuals had larger core areas that were more peripheral to campgrounds than those of highly dominant individuals, a phenomenon that was suggested by West and Peery (2017). Therefore, we theorize that subordinate individuals likely breed on the periphery of campgrounds and in effect, "commute" into campgrounds to take advantage of readily available food subsidies (see also Supplementary Figure S2). This type of "commuting" behavior to access human foods has also been observed in mammals (e.g., Tsukada 1997). While commuting jays on the periphery of campgrounds maintained similar fitness to dominant jays, individuals compelled to live even further from campgrounds may experience high energetic costs and increased exposure to predation if they frequently accessed human subsidies. These factors could reduce adult survival or affect provisioning of offspring and, subsequently, offspring quality (Ghalambor and Martin 2001; Eggers et al. 2008). Hence, jays breeding far from campgrounds likely do not make frequent foraging forays into campgrounds; and consequently, jay abundance in subsidized areas remains too low to result in density-dependent reductions in individual fecundity or body condition. This idea is also supported by the observation of West et al. (2016) that jays radio-tagged 1–2 km away from campgrounds were only rarely seen in campgrounds. Consequently, resource under-matching is maintained because dominant jays monopolize space (e.g., breeding sites) and prevent densities in campground areas from reaching the level necessary to reduce individual fitness and promote resource matching.

Adherence to an ideal despotic distribution is the most likely explanation for the persistence of resource under-matching, especially in light of the incomplete territoriality of Steller's jays (Brown 1963). However, we acknowledge that under-matching is the most observed departure from the ideal free distribution in free-living populations and can also occur due to violations of the "ideal" assumption (Kennedy and Gray 1993). Consequently, the distribution we observed could also be attributable to inability of individual jays to accurately assess habitat quality and therefore under-using high-quality habitat (i.e., because they have imperfect knowledge). While this is often the case for less mobile species (Zollner and Lima 1997; Katz and Scharf 2018), we find this scenario unlikely because jays are highly mobile and have high cognitive abilities (Emery et al. 2007), both of which should enhance their perceptual range and assist them in accurately assessing habitat conditions (Jiao et al. 2020).

While dominance is typically assumed to be positively correlated with fitness (Ellis 1995), the prevalence of readily available human food subsidies appears to have decoupled the link between dominance and fitness such that dominance does not necessarily confer a fitness benefit within campgrounds (Verhulst and Salomons 2004). Dominance is most likely to result in a fitness benefit when resources are scarce (Ellis 1995; Henderson and Hart 1995), and therefore the behavioral strategy of using aggression to maintain dominance may benefit individuals living in resource-poor landscapes, while those living in areas with abundant food subsidies do not glean a fitness benefit from this strategy. In our study site, jays likely benefitted not only from abundant human food subsidies, but also abundant natural prey items relative to what would likely be available in a heavily developed, urban area.

Our study has a few important caveats. First, jays are known to engage in a moderate level of extra-pair parentage (Overeem et al. 2014), and it is unclear how high population density may impact genetic mating systems for Steller's jays (Iossa et al. 2009; Streatfeild et al. 2011). Therefore, there could be cryptic reproductive skew towards dominant males that we were unable to measure in this study, and this could alter our assessments of individual fitness. Similarly, kinship relationships could also influence the fitness of individuals if closely related jays settle near one another (Sklepkovych 1997; Bebbington et al. 2017). Second, we measured annual fecundity primarily by considering the number of fledged young, so we may have missed any differences in mortality among dominance classes that occurred at earlier stages of nesting. For example, if dominant individuals living in areas with the most accessible human food subsidies fed more human foods to nestlings, this could have negative consequences on nestling condition and nest success (Marzluff et al. 2001; Seress et al. 2020). However, we showed that dominant and subordinate adults had similar access to human foods, which likely means nestlings of all social classes had similar access to human foods. Lastly, we were unable to measure lifetime survival and reproductive success of jays because jays are long-lived (Klimkiewicz and Futcher 1989) relative to the duration of our study. However, jays in subsidized areas have very high annual survival on average (annual survival >0.92; West et al. 2019). This suggests that even subordinate birds have a low risk of mortality and may achieve similar lifetime fecundity, considering that annual fecundity estimates were similar.

In conclusion, our results suggest that incomplete territorial exclusion could be a common mechanism explaining the high densities of synanthropic species that are often observed in subsidized habitats (Fedriani et al. 2001; Marzluff et al. 2001; Tortosa et al. 2002; Beckmann and Berger 2003; Prange et al. 2003; Olea and Baglione 2008). The "credit card hypothesis" (Shochat 2004) proposes that high densities are achieved when populations over-match human food resources, meaning that only the most dominant individuals monopolize breeding opportunities while subordinates survive and contribute to density estimates in subsidized areas without actually reproducing. While we find this hypothesis intriguing, our results, and those of Rodewald and Shustack (2008), demonstrate that synanthropes can achieve high densities in subsidized areas without over-matching food subsidies and subsequently experiencing reductions in individual fitness. Indeed, in our study, all territorial breeding individuals that utilized human food subsidies achieved elevated body condition and similar annual fecundity (see also West and Peery 2017), despite high densities in subsidized areas. Furthermore, high densities coupled with high reproduction resulting from imperfect territoriality suggest that subsidized populations may constitute source, rather than, sink populations (as proposed by Shochat 2004) that can also influence the demographics of unsubsidized areas (West et al. 2019). It is important to note, though, that this phenomenon may be more likely to occur in habitats where natural prey items that support growth and development of young, like soft-bodied arthropods, are more abundant than in urban settings. Given that urbanization continues to expand and encroach upon protected areas (Mcdonald et al. 2008; Wood et al. 2014) that provide important habitat for biodiversity (Naughton-Treves et al. 2005; Watson et al. 2014; Pacifici et al. 2020), source populations of synanthropes in subsidized areas like suburbs and campgrounds have the potential to threaten the viability of rare species using areas purportedly set aside for conservation via mechanisms like predation and competition.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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ETHICAL CONSIDERATIONS

All appropriate guidelines for humane and ethical use of animals in research were followed during capture, banding, and sampling. Research was conducted under IACUC protocol A005411-R01-A01 and scientific collection permit SC-13714.

Data Availability: Analyses reported in this article can be reproduced using the data provided by Brunk et al. (2022).

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