The dynamic nature of territoriality, transience and biding in an exploited coyote population

Authors: Morin, Dana J., and Kelly, Marcella J.

Source: Wildlife Biology, 2017(1)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00335

Wildlife Biology 2017: wlb.00335
doi: 10.2981/wlb.00335

Subject Editor: Henrik Andrén. Editor-in-Chief: Ilse Storch. Accepted 6 September 2017

The dynamic nature of territoriality, transience and biding in an exploited coyote population

Dana J. Morin and Marcella J. Kelly

D. J. Morin (danajm3@vt.edu) and M. J. Kelly, Dept of Fish and Wildlife Conservation, 106 Cheatham Hall, Virginia Tech, Blacksburg, VA 24061, USA.

Ideal despotic distribution theory and resource dispersion theory predict that individuals in populations of territorial species arrange themselves in space according to dominance and resource dispersion. When available territories are saturated, this can result in competition for preferred territories. Recently, transience in coyote populations was suggested as an advantageous life history strategy, even though transients may incur higher mortality and do not typically contribute reproductively to the population at that time. Here we assess potential types of biding, or awaiting better territory opportunities, in a highly-exploited coyote population in Virginia, USA. We used relocation data from coyotes collared from July 2011 – March 2014 to classify residents and transients based on a 95% home range area over a three-month moving window. We estimated home range stability as the distance between successive activity centers and compared it between subadults and adults. We used home range stability relative to home range area to identify extra-territorial excursions and territory turnover, or resident shifts into adjacent territories. Some coyotes adhered to the traditional form of transience, occupying very large home ranges or biding areas overlapping several resident territories, until a territory became vacant. Conversely, other individuals displayed evidence of resident territory turnover, suggesting individuals may use low quality territories as biding areas, waiting for better quality territories to become vacant. We suggest this biding population provides the capacity for rapid compensatory immigration. In response to high levels of mortality in exploited coyote populations, removal of individuals from territories may result in immediate colonization by another individual, confounding efforts to reduce overall coyote density. Thus, transience and biding may regulate population density and be a potentially advantageous life history strategy and may have implications for management of saturated populations of social predators.

Aggression and territoriality are evolutionary strategies in animal populations that maximise individual fitness by monopolising required resources for survival and reproduction (Brown 1964). However, the relationship between territoriality and resource availability is complex, as there are energetic costs and risks associated with defending territories (Carpenter 1987, Maher and Lott 2000, McLoughlin et al. 2000). In addition, the resource dispersion hypothesis suggests that the highly variable ecological costs of social groups, such as sharing of resources and reduced effective population size, determines the limits on territory and social group size, even among populations of the same species (Macdonald 1983). When the number of territories is a limiting factor in a population, this will often result in some proportion of the population without defensible territories (i.e. transients; Jaeger et al. 1996, Kamler and Gipson 2000, Perret et al. 2003, Person and Russell 2008, Hinton et al. 2012). However, these transient individuals are rarely included in population assessments, despite recent suggestions that the transient stage can be an advantageous life history strategy and contribute to population persistence (Hinton et al. 2015).

Periods of transiency can serve multiple functions in territorial social carnivores such as coyotes *Canis latrans* (Messier and Barrette 1982, Kamler and Gipson 2000). Often transients are subadults or subordinate individuals, avoiding territorial residents while waiting for opportunities to overtake existing territories (Gese et al. 1996b, Kamler et al. 2002, Hinton et al. 2015). Transience may be a transitional stage for subadults dispersing to new areas, but may also occur when former residents are displaced from defended territories (Camenzind 1978, Gese et al. 1988). Previous studies for some species such as European jays *Garrulus glandarius* (Andrén 1990), voles *Microtus* sp. (Lin and Batzli 2001), side-blotched lizards *Uta stansburiana* (Calsbeek and Sinervo 2002), and gray wolves *Canis lupus* (Person and Russell 2008) have shown decreased reproductive fitness for subordinates in larger home ranges in lower

---

quality habitats. However, because the transient phase allows individuals to continue to search for potential territories, transience could provide an advantageous life history strategy, even though reproductive opportunities may be reduced during transient periods (Camenzind 1978, Brainerd et al. 2008, Person and Russell 2008, Hinton et al. 2015).

Hinton et al. (2015) argued that the transient phase resulted in nomadic individuals occupying "biding areas", or areas where non-residents lie in wait, ready to fill vacant territories (Hinton et al. 2012, 2015). Transients are typically defined as individuals with relatively large home ranges, which overlap smaller resident territories or move through the interstitial spaces between resident territories. However, this may not be the only form of biding in highly-exploited coyote populations. There is often intense competition for territories containing more productive patches of habitat (Windberg and Knowlton 1988, Patterson and Messier 2001, Hinton et al. 2015, Morin 2015). If more productive habitats are also characterised by greater potential mortality, individual behaviour or tolerance for risk (Charnov 1976) may result in rapid territory turnover in these more productive areas, resulting in an alternative form of biding, with residents actively defending temporary territories while waiting for more productive territories to become available. Additionally, in areas with high mortality, resident coyotes may be more tolerant of yearlings remaining in natal territories for an additional year resulting in delayed dispersal (Messier and Barrette 1982, Patterson and Messier 2001, Atwood and Weeks 2003, Atwood 2006). This third, alternative form of a biding area within the resident parents' territory would minimise the associated risk of long-distance dispersal to novel areas and potentially improve survival of yearling subadults. Delayed dispersal may increase foraging efficiency of parents, alleviate reproductive costs through cooperative breeding, and reduce subadult mortality during high-risk dispersal (Bekoff et al. 1981, Moehlman 1989, Jennions and Macdonald 1994). Late-dispersing young could increase their chance of acquiring a nearby territory or their natal territory when residents are removed, likely improving reproductive fitness. All three forms of biding: transience, territory turnover, and delayed dispersal, can result in a biding population well-prepared to fill vacant territories and increase the potential for compensatory immigration as a negative feedback mechanism to mortality in density-dependent populations.

Identifying transience and biding in the social structure of a population can have important implications for management (Windberg and Knowlton 1988). The spatial structure of coyote populations, consisting of residents and transients, likely allows coyote populations to quickly rebound from temporary reductions in density (Camenzind 1978, Kamler and Gipson 2000). Density is a spatial parameter and population inputs (e.g. reproduction and immigration), can change in response to outputs (e.g. mortality and emigration). Previous studies suggested that coyote populations were density-dependent and population growth rate was positively related to prey abundance and negatively related to coyote abundance (Knowlton and Gese 1995, Windberg 1995, Knowlton et al. 1999). In particular, recruitment was limited by available territories with little recruitment when survival was high and available territories were saturated (Knowlton et al. 1999). These studies focused on reproductive recruitment and found greater reproductive rates in populations with higher mortality rates and suggested that coyote populations may be regulated by intraspecific competition through compensatory reproductive mechanisms. However, less attention has been directed towards recruitment through immigration into local populations. Recent studies have documented the ineffectiveness of culling efforts for red foxes *Vulpes vulpes* in agricultural areas in England (Baker and Harris 2006) and France (Lieury et al. 2015), and black-backed jackals *Canis mesomelas* in South Africa (Minnie et al. 2015) due to compensatory immigration across spatially-structured populations. Additionally, a meta-analysis of mesopredator removal studies found variable and largely unsuccessful results in lowering coyote populations through removals (Conner and Morris 2015). Since intensive removal efforts often demonstrate poor success in population reduction (Kilgo et al. 2014), it is likely that compensatory immigration, in addition to compensatory reproduction, plays a large role in regulating coyote populations (Kierepka et al. 2017). Therefore, determining the presence, proportion of the population, and role of biding in a coyote population can provide valuable insight into expected outcomes of management scenarios.

Ideal despotic distribution theory predicts that subordinate individuals with lower competitive capacity, such as transients, will require greater areas compared to dominant individuals (territorial residents) given equal quality in habitat (Fretwell 1972). In concordance, coyotes are often described or classified as residents or transients by overall home range size and extent of home range overlap with other territories (Kamler and Gipson 2000, Hinton et al. 2012, 2015). However, home range size can be highly variable and may differ with many factors including individual age, season, heterogeneity in resources, and local population densities, and some forms of biding may not require large home range areas, as described above. In addition, amount of aggression or degree of territoriality, often measured based on amount of intrusion or overlap among individuals in a population, is also dependent on spatial distribution of available resources (Macdonald 1983, Sacks et al. 1999, Wilson and Shivik 2011).

Our objectives were to identify residents and transients in an eastern coyote population, and to test for territory turnover and change in status (resident or transient) over time. Coyote density in our study area was very low (approximately 8 coyotes/100 km^2) but consistent across years despite low apparent survival (Morin et al. 2016) and monthly known fate survival (0.91, 0.85–0.95, or a 0.32 probability of surviving one year; Morin 2015). However, it is possible that territories, a limiting resource, were saturated, even though the population was low density and experienced high mortality, and could therefore be influenced by density-dependent processes and competition for quality territories. We expected that if territories were saturated, we would observe transients in the local population indicating competition for space and territories, common in coyote populations (Windberg and Knowlton 1988, Knowlton et al. 1999, Kamler and Gipson 2000, Hinton et al. 2015), and that transients would establish territories and residents would change territories as high quality territories became available. We also expected that subadults would be more likely to transition to and display exploratory behaviour than adults, with extra-territorial excursions leading to, or following, natal dispersal. Finally, we expected that when individuals previously identified as residents began to exhibit signs of home range instability, or movement of home range centers, relative to home range area, we would find evidence of territory turnover. In summary, we expected to find evidence of biding in the coyote population, and that coyote social status (resident or transient) is not static, but dynamic, changing quickly through time, thus providing the population capacity for compensatory immigration in response to mortality and emigration.

Methods

The study area was located primarily in western Bath County, in the Ridge and Valley region of Virginia (Fig. 1). This area incorporated approximately 43% private land (land owned by private residents and collectives such as hunt clubs), including low-density residential areas and small townships, and small-scale livestock operations and hay farms. Private land was found mostly along valley bottoms, rivers, and roadways. These private inholdings were interspersed within public lands (land owned by the public and managed by government agencies), including small state wildlife management areas and large tracts of federal land comprising the George Washington National Forest. Public land primarily consisted of mountain sides and ridgetops of contiguous, even-aged mature hardwood forests, with small clearings seeded with clover *Trifolium* sp. designed to attract wildlife. Overall, the public areas were considered to be low-productivity mature forests and provide low nutritional carrying capacity for many game species including white-tailed deer *Odocoileus virginianus* (DeCalesta 1997, Diefenbach et al. 1997).

We trapped coyotes using Victor #3 Softcatch padded foothold traps (Lititz, PA) with Paws-I-Trip pan adjustments (Homer City, PA) set to require 1.36 kg (3 lbs) of pressure to spring the trap (Association of Fish and Wildlife Agencies BMP) and free-standing non-lethal Michigan regulation coyote neck snares. Traps were checked twice per day for captures and we released all non-target captures. We physically immobilised coyotes and determined body mass, sex and estimated age based on tooth wear (Gier 1968). Coyotes estimated to be less than two years old were classified as subadults while adults were two years old or older. We fit each individual with an African Wildlife Tracking (Pretoria, South Africa) two-way satellite communication GPS collar (<3.0% of body weight) designed specifically for coyotes in

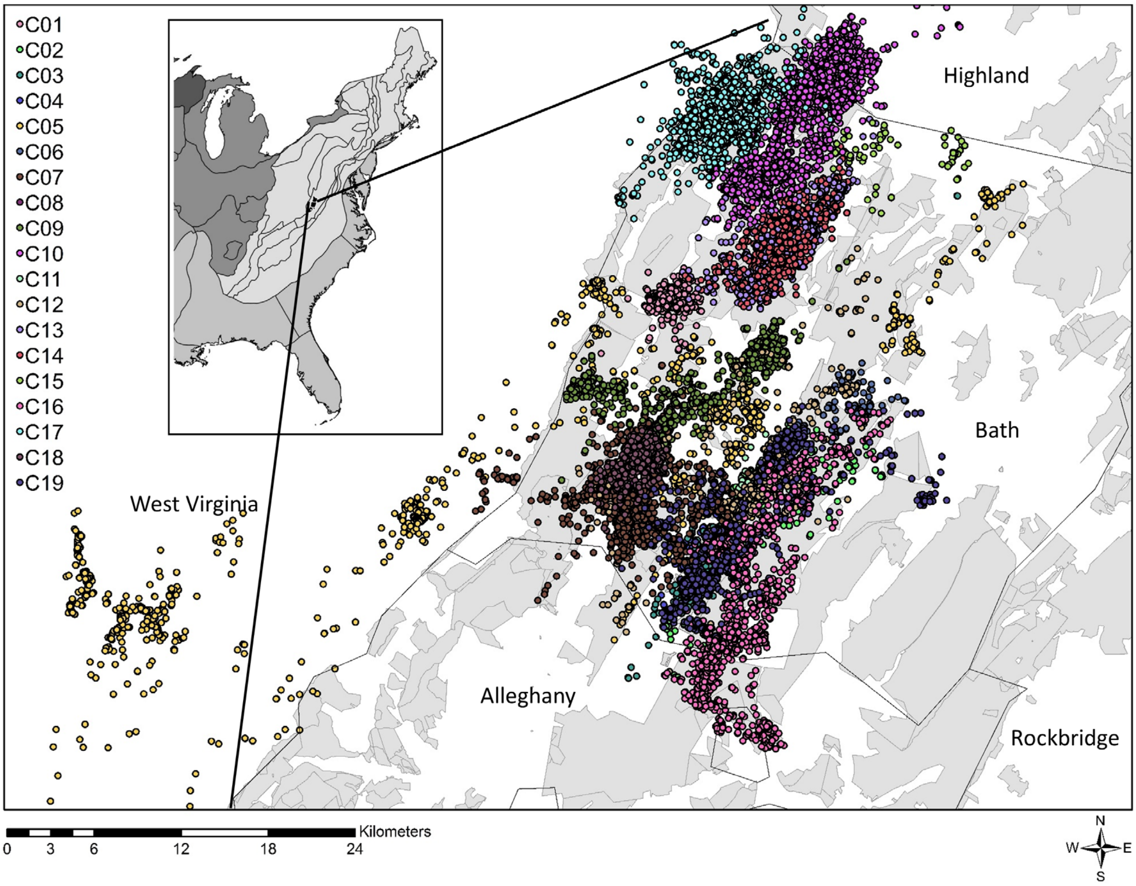

Figure 1. Study area centered in Bath County, Virginia, USA (inset), with relocations for 19 coyotes captured and tracked from July 2011 – March 2014. Relocations of some coyotes demonstrate stable territories (i.e. C14 and C17), while others occupied interstitial space between territories (i.e. C05). Light gray shading in the large map indicates public lands in Virginia, including George Washington National Forest, state wildlife management areas, and The Nature Conservancy managed Warm Springs Mountain Preserve.

our study area. We programmed collars to record four to five relocations each day on rotating schedules. Animal handling methods were approved by the Virginia Tech Institutional Animal Care and Use Committee (permit no. 10-117-FIW) and permitted by the Virginia Dept of Game and Inland Fisheries (permit no. 041503).

We evaluated three methods to describe behaviours that would indicate biding and potential for compensatory immigration. First, we tested if we could identify transients using the traditional home range area criterion. We estimated overall home range area (A) as 95% minimum convex polygons (MCP) using the adehabitat package in R (Calenge 2006, Shivik and Gese 2000, < www.r-project.org >). Although there are more sophisticated methods of estimating home range use and area, our objective was to quantify the total area defended as a territory, which is best described by 95% MCP. Coyote home range sizes can display great seasonable variability (Parker 1995) and individuals were tracked for different periods of time, so we also estimated monthly MCP area (first to the last day of each month), and MCP area over a three-month moving window (i.e. home range area for April consists of relocations from March, April and May). Second, we developed a novel method for quantifying coyote territory or home range stability based on the movement or shifting of the activity centers over time. We defined an individual's activity center (s_t) as the centroid of locations over a given time period (t), and described territory stability by the distance (d) between two successive activity centers over the defined time interval (s_t to s_{t+1}), calculated using the Pythagorean theorem ($d = \text{sqrt}(s_t^2 + s_{t+1}^2)$). Residents were assumed to have a more stable home range represented by smaller distances between successive activity centers (Royle et al. 2016) and we expected greater distances between successive activity centers with exploratory movements leading to dispersal or territory turnovers. This is similar to net squared displacement (Bunnefeld et al. 2011, Bastille-Rousseau et al. 2016), but is a more simplistic, direct model of home range stability based on displacement over specific units of time, and not units of relocations. Third, because home range size can be highly variable and monthly movement of activity centers will be relative to monthly home range size, we evaluated the ratio of distance between activity centers each month to monthly home range area at time $t\left(\dfrac{d}{A}\right)$, and expected larger values of this metric would detect resident individuals moving into adjacent territories (territory turnover) and extra-territorial excursions. For example, if an individual had a very large home range for a month, and there was subsequent large movement between activity centers from that month to the next, the ratio would be small and this movement could be expected to occur within the same large home range. However, if the distance between activity centers was much greater relative to the home range area of the initial month, the ratio would be greater and could indicate a territory turnover or large exploratory movements suggesting potential subsequent dispersal.

We performed a sensitivity analysis for the three-month moving window MCP area and the stability:area ratio to determine at what value classifications (transient or resident for the MCP area, and single territory or shifting territories for the ratio) remain consistent. We classified coyotes for each month using the metrics based on a range of possible values and defined a threshold for classification as the value at which $<1\%$ of assignments changed classification compared to the value before and the value after in the range of possible values. For example, for the stability:area ratio, we classified coyotes using a range of values between 0.1 km km^{-2} and 0.8 km km^{-2} (based on the range of possible values observed in 0.1 increments, Table 1). For each threshold value in the range, if the ratio for an individual was below the value, the coyote was considered to have a single home range. If the value for an individual was greater than the threshold, the individual was classified as experiencing an extra-territorial excursion or a territory shift in that month. We then assess the sensitivity for each value tested by calculating the number of classifications that changed compared to the value in the range immediately before it, and the value immediately after it. We repeated the sensitivity analysis for the three-month moving window MCP area over a range of 10 km^2 – 160 km^2, by 10 km^2 increments. Following this evaluation, we determined resident or transient status and territory turnover for each month a coyote was tracked using the resulting thresholds for home range area and stability:area ratio identified for the study area, and we examined increases in home range instability for indications of potential future dispersal.

To test whether subadults demonstrated greater home range instability as part of natal dispersal (Hinton et al. 2012), we log-transformed the home range stability measure to improve normality and used this as a response variable to compare two linear mixed models (LMM) using AICc (Burnham and Anderson 2002). The first model incorporated home range stability as determined only by differences among individuals (the null model) while the alternative model also included stage (i.e. subadult or adult). We fit the models using the lmer() function in the lme4 package in R (Bates et al. 2014, < www.r-project.org >). We estimated the dispersion factor ($\hat{c}$) by dividing the model deviance for the global model including all covariates by the number of residual degrees of freedom using the MuMIn package in R (Barton 2014) and compared models using AICc, or QAICc if $\hat{c} > 1$. Finally, we expected that when residents demonstrated periods of transient-like or exploratory behaviour, as reflected by home range instability relative to home range size (stability:area ratio), they transitioned to a new territory. Thus, we plotted 95% MCPs and 50% MCPs over each month to ensure that differences in locations of activity centers were in fact evidence of territory turnover and transience, and not differential use of core home range areas over time (see examples in Fig. 2 and 3).

Results

We captured and fitted collars on a total of 19 coyotes over short trapping sessions spanning two years from July 2011 to June 2013. Of the coyotes captured, eight were male (six adults ≥ 2 years of age, two subadults <2 years of age) and eleven were female (six adults and five subadults). No coyotes transitioned from subadult to adult during the

Table 1. Class structure, metric summaries, and fates of Coyotes collared in Bath County, VA, July 2011 – March 2014. Coyotes were classified as resident or transient based 95% minimum convex polygon (MCP) three-month moving window home range area ($A_{3-month}$). The stability:area ratio classification ($\frac{d}{A} = \frac{\textit{distance between successive monthly activity centers}}{95\%\ \textit{monthly MCP}}$) was used to identify territory shifts.

Coyote	Sex	Stage	Months tracked(month/year)	Overall 95% MCP area km^2	Mean monthly 95% MCP area km^2 (range)	Home range area classification ($A_{3-month}$), three-month moving window	Median distance (d) between successive activity centers km (range)	Stability:area ratio classification ($\frac{d}{A} = 0.30$ km km^{-2})	Fate
C01	F	SA	~4 (7/11 – 11/11)	8.73	5.37 (3.73 – 7.05)	resident	0.23 (0.02 – 0.45)	single territory resident	killed (recreational trapper)
C02	M	SA	~3 (8/11 – 11/11)	86.71	46.05 (7.68 – 82.71)	resident	2.29 (0.33 – 3.42)	single territory resident	killed (opportunistic shooting)
C03	F	SA	~5 (9/11 – 2/12)	22.98	17.19 (13.26 – 22.93)	resident	0.40 (0.17 – 0.49)	single territory resident	killed (recreational trapper)
C04	M	A	+1 (10/11 – 11/11)	20.79	17.92 (14.58 – 21.26)	NA	NA	NA	killed (opportunistic shooting)
C05	F	SA	~10 (10/11 – 8/12)	1277.95	140.84 (5.47 – 392.71)	transient	5.50 (1.38 – 28.89)	territory shift May 2012	killed (USDA Wildlife Services)[1]
C06	F	A	+1 (10/11 – 11/11)	22.20	17.77 (16.69 – 18.86)	NA	NA	NA	killed (opportunistic shooting)
C07[2]	M	A	~11 (4/12 – 3/13)[3]~4 (3/13 – 7/13)	104.13	24.11 (1.67 – 114.87)	resident	1.08 (0.42 – 3.46)	territory shift Mar 2013	killed (opportunistic shooting)
C08	M	A	+1 (4/12 – 5/12)	5.32	4.62 (2.30 – 6.94)	NA	NA	NA	killed (opportunistic shooting)
C09	M	SA	~8 (5/12 – 1/13)	81.32	19.96 (3.13 – 42.60)	resident	1.33 (0.19 – 8.23)	territory shift Jul[3] and Sep 2012	survived
C10[2]	F	A	~10 (5/12 – 4/13)[3]~7 (6/13 – 12/13)	79.67	42.83 (12.34 – 82.94)	resident	0.81 (0.28 – 2.59)	single territory resident	survived
C11	M	A	~1 (5/12)	8.19	NA	NA	NA	NA	killed (opportunistic shooting)
C12	F	SA	~8 (5/12 – 1/13)	216.67	70.53 (5.48 – 259.68)	resident Jun through Oct 2012, transient Dec 2012 – Jan 2013	1.90 (1.00 – 3.32)	single territory resident	killed (recreational trapper)[4]
C13	F	A	~6 (6/12 – 1/13)	56.66	34.44 (12.42 – 62.39)	resident	0.88 (0.25 – 1.97)	single territory resident	survived
C14	M	A	~7 (6/12 – 2/13)	54.37	32.30 (17.36 – 47.09)	resident	0.59 (0.10 – 1.45)	single territory resident	survived
C15	F	SA	~1 (5/13)	41.38	NA	NA	NA	NA	killed (USDA Wildlife Services)
C16	F	A	~8 (5/13 – 1/14)	159.33	65.94 (41.73 – 104.96)	transient Jun 2013, resident Jul – Nov 2013	4.27 (0.45 – 8.51)	single territory resident	survived
C17	F	A	~10 (5/13 – 3/14)	57.51	28.76 (7.32 – 71.70)	resident	1.28 (0.28 – 3.87)	single territory resident	survived[5]
C18	M	SA	~4 (5/13 – 9/13)	15.34	8.43 (0.64 – 15.21)	resident	0.33 (0.16 – 0.44)	single territory resident	killed (vehicle collision)
C19	F	SA	~8 (5/13 – 1/14)	127.08	26.00 (3.75 – 122.93)	resident Jun – Sep 2013, transient Oct – Nov 2013	1.66 (0.54 – 9.25)	territory shift Jul 2013[3] and Dec 2013	survived

[1] Reported killed by USDA Wildlife Services March 2013 after collar had stopped transmitting relocations.[2] Two individuals (C07 and C10) were captured in consecutive years and fitted with replacement collars after the first collar stopped transmitting resulting in 2 time periods when the animal was tracked.[3] Ambiguity in the results of the threshold analysis between values of 0.30 – 0.50 km km^{-2} identified extraterritorial excursions for C09, and C19. Both individuals shifted territories or dispersed that fall.[4] Collar and carcass returned by recreational trapper February 2013 after collar had stopped transmitting relocations. Reported location in a new territory.[5] Reported killed (USDA Wildlife Services) in another territory September 2016 after collar had stopped transmitting relocations.

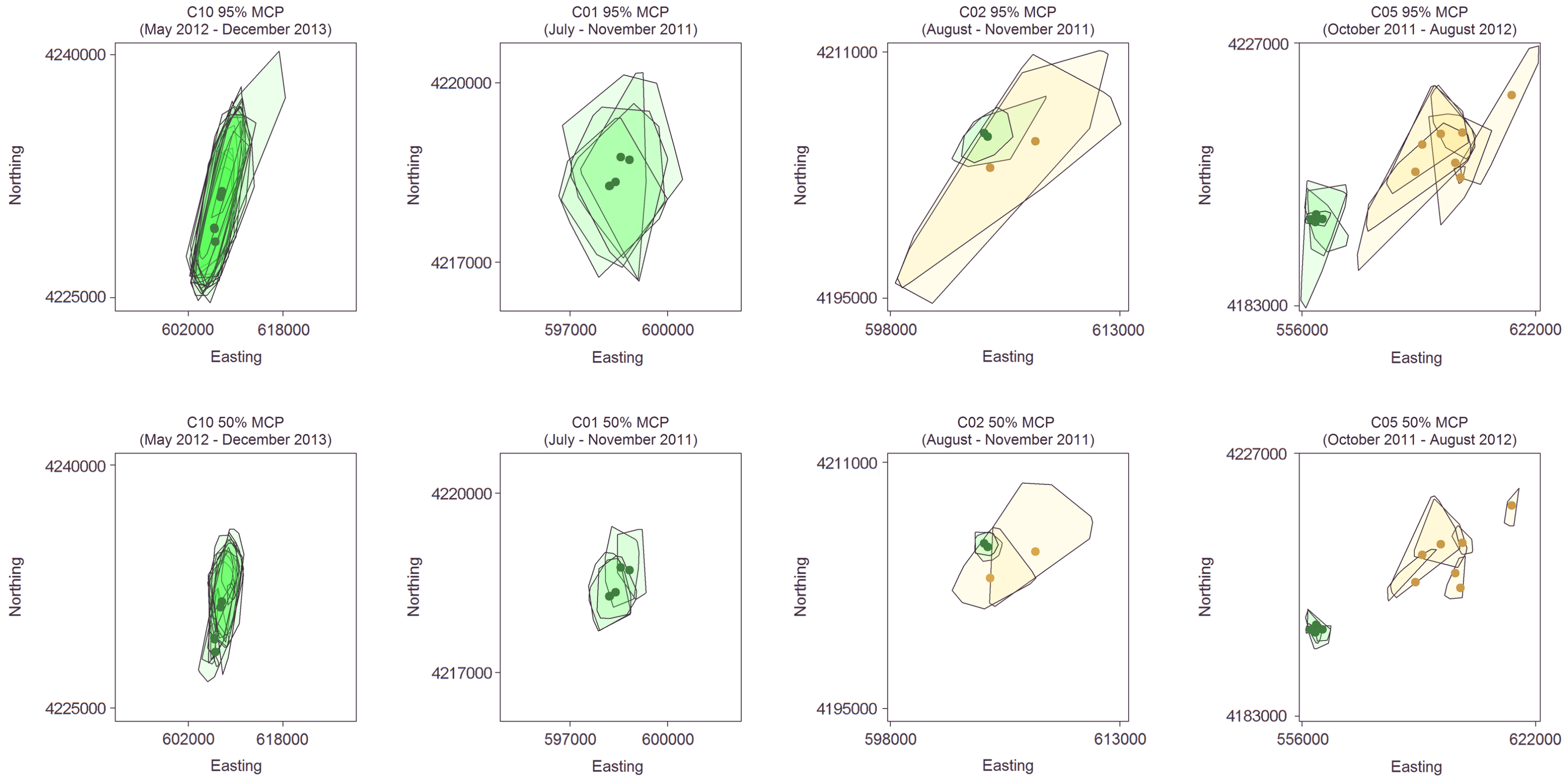

Figure 2. The 95% (top) and 50% (bottom) home range minimum convex polygons (MCPs) over one-month intervals for single territory residents (C10 and C01, green polygons), a single territory resident (C02) the begins to display large exploratory movements (gold polygons), and a transient that eventually establishes a territory (green polygons) outside the study area (C05). The points represent the activity centers (centroid of all locations) for each month a coyote was tracked. The x- and y-axes are UTM coordinates (NAD 1927) and scaled to the size of each individual's home range.)

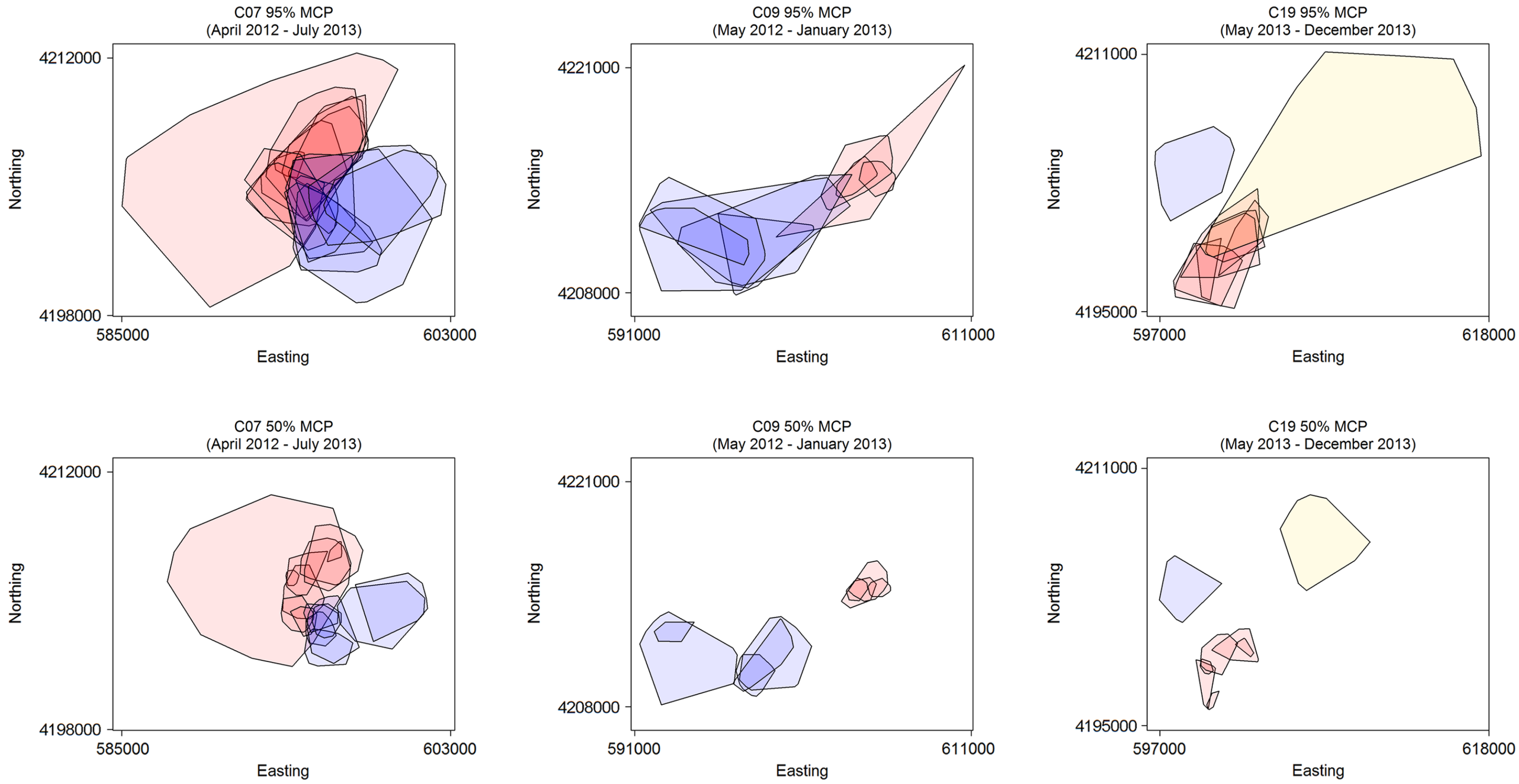

Figure 3. The 95% (top) and 50% (bottom) home range minimum convex polygons (MCPs) polygons over one-month intervals for three individuals that demonstrate territory turnover. C07 (left) was a single territory resident for one year (red polygons), from when first collared in April 2012 – March 2013 when it shifted to a second adjacent territory to the west (blue polygons), which it maintained until killed in July 2013. C09 maintained a single territory from when collared in May 2012 until September 2012 (red polygons), when it shifted to an adjacent territory to the east (blue polygons) where it remained until the collar stopped transmitting locations in January 2013. C19 maintained a single territory (red polygons) from May 2013 until November 2013 when it displayed a large exploratory movement (gold polygon), and then appeared to establish a second territory (blue polygon) in December 2013 before the collar stopped transmitting locations. The x- and y-axes are UTM coordinates (NAD 1927) and scaled to the size of each individual's home range.

time their collars were active. Coyote mortality was very high in the study area and 63% of coyotes were killed during the time they were tracked with a collar. One individual was hit by a vehicle, three were killed by recreational trappers, six were shot, and two were killed by authorised devices used by US Dept of Agriculture, Wildlife Services, to reduce potential damage to livestock. Collars were operational on individual coyotes over different intervals from July 2011 through March 2014. Tracking duration ranged from one month (four coyotes were killed within approximately one month of initial capture) to 16 months for a male (C07) and 18 months for a female (C10), both of whom were recaptured in successive years and fitted with new collars.

Overall 95% MCP monthly home range area ranged from 2.30–392.71 km^2 (mean = 41.54 km^2) (Fig. 4). The sensitivity analysis of the 95% MCP three-month moving window metric demonstrated <0.01 change in classifications when residents were classified with <120 km^2 home range area and transients were classified with >120 km^2 home range area (Fig. 5). Based on this threshold, one individual, a subadult female (C05), was classified as a transient for the duration of tracking (Table 1). One individual was classified as a transient when first collared (C16: an adult female collared in May 2013), and then established a territory for the remainder of the study. Two other individuals (C12 and C19, both subadult females) were initially classified as residents and transitioned to transience before the end of the study.

The stability metric, distance between successive activity centers, indicates several different types of behaviour. Some individuals maintained consistent, stable home ranges (see C10 and C01 in Fig. 2 and 4), However, other individuals showed varying degrees of activity center instability over time (Fig. 4). When home range instability is considered relative to overall home range area (stability:area ratio), sensitivity analysis suggests a 0.30 km km^{-2} threshold for extra-territorial excursions and territory turnover among residents. However, there is some ambiguity between 0.30 and 0.50 km km^{-2}, an artifact of defining a threshold for classification of a continuous variable, especially when sample sizes are small and the data is highly variable, that results in a change of classifications for two individuals in single months that are on the border of the 0.3 threshold (Fig. 5, Supplementary material Appendix 1 Table 1A). Based on the 0.30 km km^{-2} threshold, the metric accurately describes territory turnover for three individuals: C07 in March 2013, C09 in September 2012, and C19 in December 2013 (Fig. 3). In addition, the 0.30 km km^{-2} threshold also identified two extended extraterritorial excursions (C09 in July 2012 and C19 in July 2013) for individuals that ultimately moved to different territories.

Using the log-transformation of distance between home range centers did not provide strong support for differences in home range stability by stage (adult or subadult). The model including stage as an explanatory variable (ΔAICc = 2.10, ω = 0.259, AICc = 342.10, n = 180, groups = 18, logLikelihood = –166.9, residual degrees of freedom = 114) received less

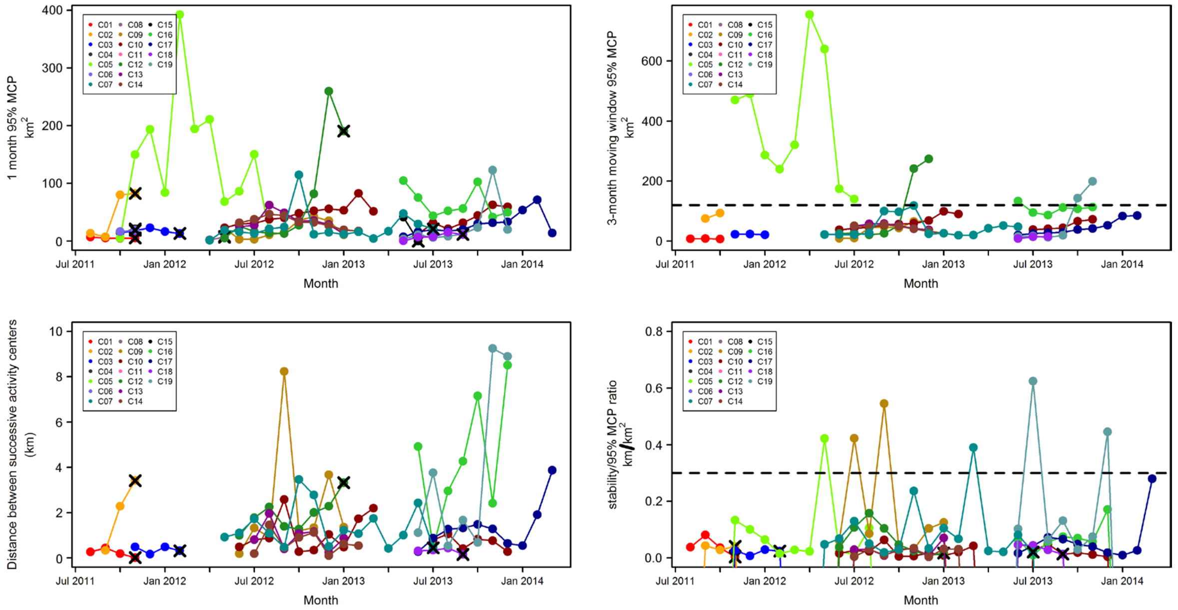

Figure 4. Longitudinal plots of monthly 95% minimum convex polygon (MCP) home range area (top left), three-month moving window 95% MCP home range area (top right) where the dashed line represents the selected threshold (120 km^2) for classifying residents from transients, distance between successive activity centers, a measure of home range stability over time (bottom left), and the stability:area ratio classification $\left(\frac{d}{A}=\frac{\textit{distance between successive monthly activity centers}}{95\%\ \textit{monthly MCP}}\right)$, where the dashed line represents the selected threshold (0.30 km km^{-2}) for identifying territory turnover. Each colored line represents 1 of 19 coyotes tracked, a black 'X' indicates when a coyote was killed. When coyotes were killed and the time interval was too short to calculate a metric they are not included in the plot. C05, a transient with a large home range, is not included in the plot of distance between successive activity centers as the values far exceed the y-axis limits.

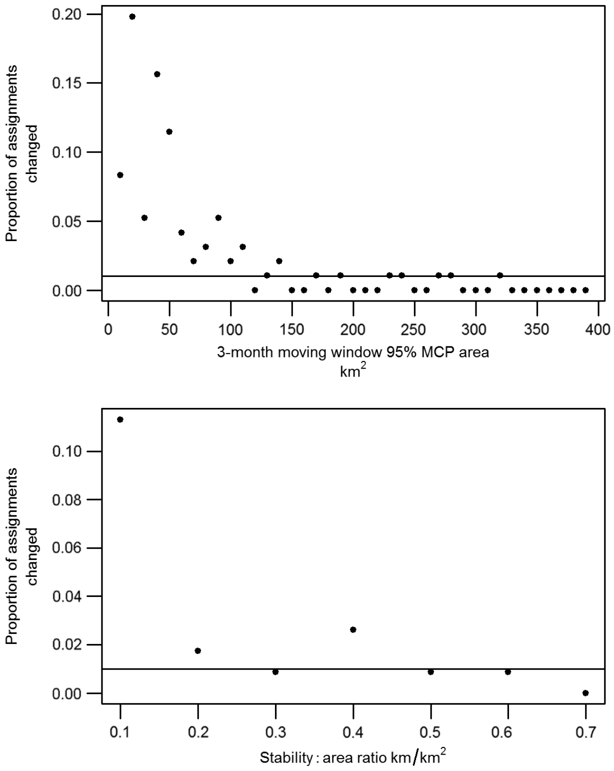

Figure 5. Sensitivity analysis plots for three-month moving window 95% MCP home range area (top) and the stability:area ratio $\left(\frac{d}{A}=\frac{\textit{distance between successive monthly activity centers}}{95\%\ \textit{monthly MCP}}\right.$, bottom). The x-axis is the range of possible values tested as a classification threshold (in 10 km^2 increments for three-month moving window 95% MCP home range area, and 0.1 km km^{-2} increments for the stability:area ratio). The y-axis is the proportion of assignments that changed classification when the threshold was changed by one increment. Both metrics were summarized at one-month intervals and thresholds were selected that resulted in < 0.01 changes in classification compared to the previous value across a range of possible values.

support than the null model, which included only individual variability (ΔAICc = 0, ω = 0.741, AICc = 340.00, n = 180, groups = 18, logLikelihood = –166.9, residual degrees of freedom = 115). However, there was a much wider range in subadult home range stability as measured by distance between activity centers (0.02–28.89 km) compared to adults (0.10–8.51 km). Mean distance between activity centers in successive months was much greater for subadults (3.60 km) compared to adults (1.60 km). The medians for subadults (1.27 km) and adults (1.07 km) were much more similar, suggesting subadult female (C05), a transient that eventually dispersed to a neighboring county, was exceptional. When C05 is not considered, mean distance between activity centers for subadults was smaller (1.71 km) and home range stability was more similar between subadults and adults as suggested by the LMM results.

Discussion

We found evidence of transients, extraterritorial excursions, dispersal and resident territory turnover in a highly-exploited coyote population. Transients covered large areas actively attempting to disperse. However, presence of territory turnover suggests residents may also compete for, or fill, vacant high-quality territories and can respond quickly when other residents are removed (Gese 1998, 2001; Sacks et al. 1999). The metrics we used allowed us to identify and describe the transient and biding dynamics that likely allow for rapid local recruitment in response to high mortality and possible population regulation through compensatory local immigration (Kierepka et al. 2017). These findings suggest transience and biding may be potentially advantageous life history strategies for highly-exploited populations and may confound population management objectives.

We identified an adult resident population maintaining single territories as demonstrated by very consistent monthly 95% MCP home ranges and small distances between successive activity centers, even though core use areas may have changed seasonally (see C10 in Fig. 2 for an example). It is possible these individuals were defending desirable territories and not attempting to shift into neighboring territories. Other individuals showed signs of biding and attempts to shift into new territories. Unequal territory quality and access to resources can be an important determinant of both territory size and social structure in social canids (Tallents et al. 2012), and influence forays and movement into other territories (Wilson and Shivik 2011). Extra-territorial excursions have been documented across a variety of taxa despite the inherent danger of intruding on a foreign territory (Double and Cockburn 2000, Patterson and Messier 2001). Presumably the risk is motivated by an advantage not obtained by remaining in one's territory. Extra-territorial excursions in mammals have been described for gray wolves (Walton et al. 2001), red fox (Tsukada 1997), black-backed jackals (Kaunda 2001), and feral cats *Felis catus* (Mcgregor et al. 2016) in response to superior food resource opportunities, and by gray wolves (Fuller et al. 1989), Eurasian lynx *Lynx lynx* (Vogt et al. 2014), slender-tailed meerkats *Suricata suricata* (Doolan and Macdonald 1996), roe deer *Capreolus capreolus* (Debeffe et al. 2014), and white-tailed deer (Karns et al. 2011) to increase reproductive opportunity (temporary excursions) or reduce inbreeding (permanent dispersal from natal area). In addition, extra-territorial excursions can increase during periods of low prey density for spotted-hyenas *Crocuta crocuta* (Honer et al. 2005) and gray wolves (Messier 1985), and may be more common for individuals of lower social status (Gese et al. 1996b, Honer et al. 2005). Thus, it is possible territory transitions, detectable at the one-month resolution, may have been the result of residents being displaced from a territory by a more dominant individual or group, or residents motivated to shift into a better territory that becomes vacant when the territory holder was removed through mortality (Sacks et al. 1999, Gese 2001), potentially improving access to resources including food and mates.

Biding in our study area occurred throughout the year with extraterritorial excursions and territory shifts occurring in March, May, July, September and November. Additionally, both adults and subadults were identified as transients and shifted territories and we did not detect a difference in home range stability between subadults and adults. As such, it does not appear that biding in this population is dependent on season, age or reproductive stage, but is instead dependent on the individual or territory quality and possibly driven by restricted access to concentrated distribution of sparse resources (Geese et al. 1996a).

Traditionally the transient phase, defined by a large biding area, was considered a transitional stage following natal dispersal while individuals sought out available territories (Camenzind 1978, Kamler and Gipson 2000, Hinton et al. 2015). We identified one subadult female that behaved as a large-ranging transient for most of the time tracked, then it appeared to establish a possible territory in Greenbrier County, West Virginia, before being killed in that area by USDA Wildlife Services. In addition, two individuals transitioned from resident to transient based on the area of the three-month 95% MCP, in late fall and winter (Fig. 4), the season typically associated with natal dispersal (Harrison 1992, Gese et al. 1996b). Intraspecific competition, social structure, and disparity in resource availability add complexity to the local coyote population dynamics, possibly providing resiliency to high levels of mortality. The presence of transients, residents displaying biding behaviour, and territory turnover found in our study area demonstrate that local coyote populations may be spatially prepared to quickly replace individuals removed in the study area (Windberg and Knowlton 1988). As a result, the high mortality rate and competition for resources in our study area may have resulted in several different types of biding strategies.

Delayed dispersal may also complicate population management objectives and actions. We did not capture or track any individuals estimated under 1 years of age, the typical age of juvenile coyote dispersal (Harrison 1992). Yet we still documented several exploratory movements that suggest dispersal attempts by subadults, potentially from a natal area (C02, C12 and C19). Two of these were confirmed killed outside of their established territories (C02 and C12), and the fate of the third is unknown as the collar stopped functioning. Dispersing individuals are commonly vulnerable to harvest (Harrison 1986) and intraspecific aggression (Bekoff 1978), creating a situation where breeding residents may tolerate related yearlings, resulting in increased sociality and group size (Messier and Barrette 1982, Patterson and Messier 2001). Delayed dispersal has been reported for social canid species (Bekoff et al. 1981) including red wolves *Canis rufus* (Sparkman et al. 2011) and gray wolves (Gese and Mech 1991), and could result in increased group size within territories if relative resource availability increased with local mortality. This could create a third potential biding population prepared to annex or subsume adjacent or natal territories when residents are removed. Delayed dispersal may also explain why we did not detect a difference in subadult and adult home range stability. Subadult individuals may have opted to remain relatively safe, behaving as residents within stable natal territories for an additional year.

The complex and adaptable spatial and social structure of canids should be considered when assessing possible management scenarios, especially as the life-stage of individuals comprising the biding population appears to change with mortality rates (Gese 1998, Person and Russell 2008) and may alter future reproductive potential across populations. For example, Gese et al. (1988) found yearlings and very old coyotes comprised >68% of the transient population. Older coyotes have very little reproductive potential and yearlings tended to have lower survival, suggesting neither group are likely to contribute to the future population (Fisher 1958). In addition, in a similar study on another social canid species (gray wolves), very few transient wolves had the opportunity to take over vacant territories, and therefore did not likely contribute reproductively (Person and Russell 2008). However, both of these populations had relatively low mortality rates compared to the population in our study area. We found subadults were no more likely to display home range instability than adults and there were not many older coyotes detected in the population, possibly due to the very high mortality rate in our study (Knowlton and Gese 1995). Thus, the local compensatory immigrant population, motivated by access to territories with high value resources, could be composed of individuals biding in lower quality or natal territories, not necessarily just yearlings and older coyotes. As a result, it is possible the high harvest rate could change not only the age class structure of the population, but also result in increased reproductive potential of the transient or biding population (Knowlton and Gese 1995, Windberg 1995).

While we observed multiple forms of potential biding as described by the evaluated metrics, there are limitations to this study. Sample sizes were small, as is common in telemetry studies of low-density, widely dispersed populations. In addition, as mortality was high, several individuals were only tracked for 1–2 months before being killed and we were unable to estimate metrics for these individuals, or observe a resident enter the transient phase and confirm complete dispersal to a new territory. Finally, we only consider data from a single population over 3.5 years, and did not compare populations with different levels of mortality or changing mortality over time. As a result, inference from our study is limited, but suggests several lines of inquiry that would be critical for future research and a better understanding of how social aggression, resource dispersion, and mortality influence transience, biding, and compensatory immigration. The metrics described are based on MCPs and distance between centroids of relocations over time, and can be easily implemented and compared across previous and future studies. The presence and form of the biding population, the proportion of the total population, and age class composition of transients and biding individuals can be highly variable across populations. Thus further research directly assessing the role of transience and biding in populations dynamics is needed to allow for better informed decisions regarding coyote management.

In our study population, mortality was high and the region is comprised of known differences in habitat quality and associated resources between mature forests along mountain slopes and ridgelines compared to more productive narrow valley bottoms with agricultural fields and pastures (Bowersox and Ward 1972, Morin 2015). However, we expect that in saturated populations with higher resident survival including no exploitation or harvest (Windberg 1995, Knowlton et al. 1999), residents would maintain and defend consistent territories and home range instability would decrease and only be detectable during the fall and winter seasons when individuals defend territories from immigrants, search for mating opportunities, and subadults emigrate. We also expect that home range stability would decrease with a more homogeneous distribution of resources and low disparity in territory quality, as there would be decreased motivation to risk a move to an unknown, potentially more dangerous territory. Thus, assessing home range stability may be a useful metric for quantifying the compensatory immigration potential within a population, but comparisons with populations experiencing different levels of mortality and resource availability is required.

Coexistence among competitors can be facilitated by spatial heterogeneity in distribution of competitors, resources, and competition refuges (Durant 1998). Although this interaction is often described at the scale of a multispecies community of competitors, the complex social structure of territorial canid populations may also allow for competition refuges in the form of differing resident and transient space use dynamics (Kamler and Gipson 2000, Hinton et al. 2015). Although individuals in the transient life-stage may not be reproductively active, the coexistence of residents and transients provides population benefits by maintaining population density through territory turnover, particularly in highly-exploited populations. Thus, our results suggest biding in exploited coyote populations could be an advantageous life history strategy (Hinton et al. 2015).

As coyote density was consistent in the region during the length of the study (Morin et al. 2016), our lines of evidence for transience and biding suggest a spatially structured population capable of rapid recruitment and population regulation through compensatory local immigration. Therefore, local coyote control efforts (e.g. bounties, lotteries, and predator calling contests) should not be expected reduce local coyote populations, minimise potential impacts to prey species, or mitigate potential human–coyote conflicts, even over short time intervals, if resident coyotes that are removed are immediately replaced with individuals in a biding state (Baker and Harrison 2006, Lieury et al. 2015). However, territorial behaviour and territory turnover suggest that local coyote populations are regulated through competition for space and territories, similar to findings of previous studies of established coyote populations in the western USA (Knowlton and Gese 1995). In these studies, lightly exploited populations exhibited boundedness (Murdoch 1994) where recruitment was highly limited by available territories and 'reproductive rates fell far short of the biotic potential of the species' (Knowlton and Gese 1995). Thus, it is not surprising that current removal rates do not reduce population numbers (Conner and Morris 2015). In fact, coyote populations appear to be increasing or are stable in Virginia (Virginia Dept of Game and Inland Fisheries 2012, USDA 2013), possibly because attempted broad scale removals are reducing or negating the effects of intraspecific competition as a regulation mechanism. As a result, transience and biding in territorial carnivores may allow for population persistence, particularly when exploitation is spatially inhomogeneous and densities and resources are also variable.

Acknowledgements – We would like to thank collaborators Robert Alonso, the Virginia Dept of Game and Inland Fisheries, including Mike Fies, Dave Steffen, Al Bourgeois and Nelson Lafon, US Forest Service, including Steve Tanguay, Carol Croy, the Nature Conservancy and Marek Smith at the Warm Springs Mountain Preserve. In addition, we thank Mike Cherry, Mike Conner and Jim Nichols for invaluable discussions.
Funding – Financial support provided by the Virginia Dept of Game & Inland Fisheries came from the US Fish and Wildlife Service through the Wildlife and Sport Fish Restoration Program, Project WE99R. Finally, we appreciated additional funding and support from the Appalachian members of the Virginia Deer Hunter Association, The Nature Conservancy, the Edna Bailey Sussman Foundation, and the Cunningham Fellowship (Virginia Tech Graduate School).
Permits – Animal handling methods were approved by the Virginia Tech Institutional Animal Care and Use Committee (permit #10-117-FIW) and permitted by the Virginia Department of Game and Inland Fisheries (permit #041503).

References

Andrén, H. 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay (*Garrulus glandarius* L.). – Ecology 71: 1796–1803.
Atwood, T. C. 2006. The influence of habitat patch attributes on coyote group size and interaction in a fragmented landscape. – Can. J. Zool. 84: 80–87.
Atwood, T. C. and Weeks, Jr, H. P. 2003. Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. – Can. J. Zool. 81: 1589–1597.
Baker, P. J. and Harris, S. 2006. Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? – Eur. J. Wildl. Res. 52: 99–108.
Barton, K. 2014. MuMIn: multi-model inference. – R package ver. 1.12.1. <http://CRAN.R-project.org/package=MuMIn>.
Bastille-Rousseau, G. et al. 2016. Flexible characterization of animal movement pattern using net squared displacement and a latent state model. – Movement Ecol. 4: 15.
Bates, D. et al. 2014. lme4: Linear mixed-effects models using eigen and S4. – R package ver. 1.1-7, <http://CRAN.R-project.org/package=lme4>.
Bekoff, M. 1978. Coyotes : biology, behaviour and management, 2nd edn. – Academic Press.
Bekoff, M. et al. 1981. Life-history patterns and sociality in canids: body size, reproduction and behavior. – Oecologia 50: 386–390.
Bowersox, T. W. and Ward, W. W 1972. Prediction of oak site index in the ridge and valley region of Pennsylvania. – For. Sci. 18: 192–197.
Brainerd, S. M. et al. 2008. The effects of breeder loss on wolves. – J. Wildl. Manage. 72: 89–98.
Brown, J. L. 1964. The evolution of diversity in avian territorial systems. – Wilson Bull. 76: 160–69.
Bunnefeld, N. et al. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. – J. Anim. Ecol. 80: 466–476.
Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information theoretic approach, 2nd edn. – Springer.
Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. – Ecol. Model. 197: 516–519.
Calsbeek, R. and Sinervo, B. 2002. An experimental test of the ideal despotic distribution. – J. Anim. Ecol. 71: 513–523.
Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. – In: Bekoff, M.

(ed.), Coyotes: biology, behavior and management. Academic Press, pp. 267–294.

Carpenter, F. L. 1987. Food abundance and territoriality: to defend or not to defend? – Am. Zool. 27: 387–399.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. – Theor. Popul. Biol. 9: 129–136.

Conner, L. M. and Morris, G. 2015. Impacts of mesopredator control on conservation of mesopredators and their prey. – PloS One 10: e0137169.

Debeffe, L. et al. 2014. A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. – Oecologia 176: 431–443.

DeCalesta, D. S. 1997. Deer and ecosystem management. – In: McShea W. J. et al. (eds), The science of overabundance: deer ecology and population management. Smithsonian Inst. Press, pp. 267–279.

Diefenbach, D. R. et al. 1997. Attitudes of Pennsylvania sportsmen towards managing white-tailed deer to protect the ecological integrity of forests. – Wildl. Soc. Bull. 25: 244–251.

Doolan, S. P. and Macdonald, D. W. 1996. Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricatta suricatta*) in the southwestern Kalahari. – J. Zool. 240: 59–73.

Double, M. and Cockburn, A. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. – Proc. R. Soc. B 267: 465–470.

Durant, S. M. 1998. Comparative refuges and coexsistence: an example from Serengeti carnivores. – J. Anim. Ecol. 67: 370–386.

Fisher, R. 1958. The genetical theory of natural selection. – Dover Publications.

Fretwell, S. D. 1972. Populations in a seasonal environment. No. 5. – Princeton Univ. Press.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. – Wildl. Monogr 105: 3–41.

Gese, E. M. 1998. Response of neighboring coyotes (*Canis latrans*) to social disruption in an adjacent pack. – Can. J. Zool. 76: 1960–1963.

Gese, E. M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, when and why. – Can. J. Zool. 79: 980–987.

Gese, E. M. and D. L. Mech. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. – Can. J. Zool. 69: 2946–2955.

Gese, E. M. et al. 1988. Home range and habitat use of coyotes in southeastern Colorado. – J. Wildl. Manage. 52: 640–646.

Gese, E. M. et al. 1996a. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. – Can. J. Zool. 74: 769–783.

Gese, E. M. et al. 1996b. Social and nutritional factors influencing the dispersal of resident coyotes. – Anim. Behav. 52: 1025–1043.

Gier, H. T. 1968. Coyotes in Kansas. – Kansas State College Agric. Exp. Stn Bull 393: 1–118.

Harrison, D. J. 1986. Coyote dispersal, mortality, and spatial relationships with red foxes in Maine. – Univ. of Maine.

Harrison, D. J. 1992. Dispersal characteristics of juvenile coyotes in Maine. – J. Wildl. Manage. 56: 128–138.

Hinton, J. W. et al. 2012. Long-distance movements of transient coyotes in eastern North Carolina. – Am. Midl. Nat. 168: 281–288.

Hinton, J. W. et al. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). – PloS One 10: e0132203.

Honer, O. P. et al. 2005. The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. – Oikos 108: 544–554.

Jaeger, M. M. et al. 1996. Seasonal differences in territorial behavior by golden jackals in Bangladesh: howling versus confrontation. – J. Mammal. 77: 768–775.

Jennions, M. D. and Macdonald, D. W. 1994. Cooperative breeding in mammals. – Trends Ecol. Evol. 9: 89–93.

Kamler, J. F. and Gipson, P. S. 2000. Space and habitat use by resident and transient coyotes. – Can. J. Zool. 78: 2106–2111.

Kamler, J. F. et al. 2002. Improved trapping methods for swift foxes and sympatric coyotes. – Wildl. Soc. Bull. 30: 1262–1266.

Karns, G. R. et al. 2011. Investigation of adult male white-tailed deer excursions outside their home range investigation of adult male white-tailed deer excursions outside their home range. – Southeastern Nat. 10: 39–52.

Kaunda, S. K. K. 2001. Spatial utilization by black-backed jackals in southeastern Botswana. – Afr. Zool. 36: 143–152.

Kierepka, E. M. et al. 2017. Effect of compensatory immigration on the genetic structure of coyotes. – J. Wildl. Manage., in press, doi: 10.1002/jwmg.21320.

Kilgo, J. C. et al. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. – J. Wildl. Manage. 78: 1261–1271.

Knowlton, F. F. and Gese, E. M. 1995. Coyote population processes revisited. – In: Coyotes in the southwest: a compendium of our knowledge. Symposium Proceedings, pp. 1–6.

Knowlton, F. F. et al. 1999. Coyote depredation control: an interface between biology and management. – J. Range Manage. 52: 398–412.

Lieury, N. et al. 2015. Compensatory immigration challenges predator control: an experimental evidence-based approach improves management. – J. Wildl. Manage. 79: 425–434.

Lin, Y. K. and Batzli, G. O. 2001. The influence of habitat quality on dispersal, demography and population dynamics of voles. – Ecol. Monogr. 71: 245–275.

Macdonald, D. W. 1983. The ecology of carnivore social behavior. – Nature 301: 379–383.

Maher, C. R. and Lott, D. R. 2000. A review of ecological determinants of territoriality within vertebrate species. – Am. Midl. Nat. 143: 1–29.

Mcgregor, H. W. et al. 2016. Extraterritorial hunting expeditions to intense fire scars by feral cats. – Sci. Rep. 6: 22559.

McLoughlin, P. D. et al. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. – Evol. Ecol. 14: 39–60.

Messier, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. – Can. J. Zool 63: 239–245.

Messier, F. and Barrette, C. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. – Can. J. Zool. 60: 1743–1753.

Minnie, L. et al. 2015. Compensatory life history responses of a mesopredator may undermine carnivore management efforts. – J. Appl. Ecol. 53: 379–387.

Moehlman, P. D. 1989. Intraspecific variation in canid social systems. – In: Gittleman, J. L. (ed.), Carnivore behavior, ecology and evolution. Springer, pp. 143–163.

Morin, D. J. 2015. Spatial ecology and demography of eastern coyotes (*Canis latrans*) in western Virginia. – Virginia Tech.

Morin, D. J. et al. 2016. Monitoring coyote population dynamics with fecal DNA and spatial capture–recapture. – J. Wildl. Manage. 80: 824–836.

Murdoch, W. W. 1994. Population regulation in theory and practice. – Ecology 75: 271–287.

Parker, G. R. 1995. Eastern coyote: the story of its success. – Nimbus Publishing.

Patterson, B. R. and Messier, F. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. – J. Mammal. 82: 463–477.

Perret, N. et al. 2003. Transience, dispersal and survival rates in newt patchy populations. – J. Anim. Ecol. 72: 567–575.

Person, D. K. and Russell, A. L. 2008. Correlates of mortality in an exploited wolf population. – J. Wildl. Manage. 72: 1540–1549.

Royle, J. A. et al. 2016. Spatial capture–recapture models allowing Markovian transience or dispersal. – Popul. Ecol. 58: 53–62.

Sacks, B. N. et al. 1999. Territoriality and breeding status of coyotes relative to sheep predation. – J. Wildl. Manage. 63: 593–605.

Shivik, J.A. and Gese, E. M. 2000. Territorial significance of home range estimators for coyotes. – Wildl. Soc. Bull. 28: 940–946.

Sparkman, A. M. et al. 2011. Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). – Behav. Ecol. 22: 199–205.

Tallents, L. A. et al. 2012. Territory quality determines social group composition in Ethiopian wolves *Canis simensis*. – J. Anim. Ecol. 81: 24–35.

Tsukada, H. 1997. A division between foraging range and territory related to food distribution in the red fox. – J. Ethol. 15: 27–37.

USDA. 2013. Status of the Virginia Cooperative Coyote Damage Control Program, Fiscal Year 2013. – US Dept Agric.

Virginia Department of Game and Inland Fisheries 2012. Virginia bowhunter survey, hunter harvest, and pelt harvest data. – Virginia Dept of Game and Inland Fisheries.

Vogt, K. et al. 2014. Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. – Behav. Processes 106: 98–106.

Walton, L. R. et al. 2001. Movement patterns of barren-ground wolves in the central Canadian arctic. – J. Mammal. 82: 867–876.

Wilson, R. R. and Shivik, J. A. 2011. Contender pressure versus resource dispersion as predictors of territory size of coyotes (*Canis latrans*). – Can. J. Zool. 89: 960–967.

Windberg, L. A. 1995. Demography of a high-density coyote population. – Can. J. Zool. 73: 942–954.

Windberg, L. A. and Knowlton, F. F. 1988. Management implication of coyote spacing patterns in southern Texas. – J. Wildl. Manage. 52: 632–640.

Supplementary material (available online as Appendix wlb-00335 at <www.wildlifebiology.org/appendix/wlb-00335>). Appendix 1.