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Coyotes living near cities are bolder: implications for dog evolution and human-wildlife conflict

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Abstract

How animal populations adapt to human modified landscapes is central to understanding modern behavioural evolution and improving wildlife management. Coyotes (*Canis latrans*) have adapted to human activities and thrive in both rural and urban areas. Bolder coyotes showing reduced fear of humans and their artefacts may have an advantage in urban environments. We analysed the reactions of 636 coyotes to novel human artefacts (camera traps) at 575 sites across the state of North Carolina. Likelihood of a coyote approaching the camera increased with human housing density suggesting that urban coyotes are experiencing selection for boldness and becoming more attracted to human artefacts. This has implications for both human-wildlife conflict and theories of dog domestication. We also note physical traits in coyotes that could be the result of domestication-related selection pressures, or dog hybridization.

Keywords

self-domestication, urban evolution, coyote wildlife management, urban coyotes, coyote boldness, human-wildlife conflict.

1. Introduction

The degree to which a species can adapt their behaviour to human-modified environments might be the most critical survival trait in the Anthropocene (Tuomainen & Candolin, 2011; Lowry et al., 2013; Sol et al., 2013; Honda et al., 2018). Harvest or persecution by humans is one of the most im-

portant causes of mortality for many species (Hill et al., 1987; Collins & Kays, 2011), resulting in some of the strongest evolutionary selection pressures ever measured (Darimont et al., 2009) and declining populations for those species that do not adapt (Schipper et al., 2008). Species that evolve to dynamically adjust their behaviour to match local threats benefit from shy behaviour in risky areas, but might also encounter selection for more bold behaviours in safe areas where they could encounter other benefits from living near people such as increased food availability or reduced predation from larger predators (Berger, 2007; Parsons et al., 2018).

Human modification of environments induces diverse changes in wildlife behaviour (Sih et al., 2010; Samia et al., 2015; Sullivan et al., 2017), and in particular the process of wild animals evolving to become attracted to humans has recently been invoked to explain how some species were initially domesticated (Trut et al., 2009; Hare, 2017). In the case of dogs, the self-domestication hypothesis (SDH) posits that wolves in the Pleistocene were at an adaptive advantage if they were able to approach and use the new ecological niche created with humans living at higher densities in the late Pleistocene (Hare & Tomasello, 2005; Hare, 2017). Experimental selection of foxes for attraction to humans, instead of responding with fear or aggression, has also been shown to lead to incidental by-products including blue eyes, white tail tip, and increased skill at using human social cues (Trut, 1999; Hare et al., 2005). These morphological, behavioural, and cognitive traits are associated with domestication but were not under direct selection themselves (Trut, 1999; Dugatkin & Trut, 2017). According to this model, it is only very recently in the Holocene that a second stage of domestication occurred in which humans intentionally bred dogs through artificial selection (Wobber et al., 2009).

There are numerous examples of other species adapting to thrive near people. While there is considerable variation in response to urbanization across species and contexts (see Bonier, 2012) for a review of endocrine responses in birds), there are several examples demonstrating the possibility that in some cases urbanization can result in traits strikingly similar to those seen in the farm fox experiment and modern domesticated species. Key deer (*Odocoileus virginianus clavium*) living in areas with higher human population densities are larger, more social and have higher reproductive success (Harveson et al., 2007). Urban black birds are less aggressive, have lower

cortisol levels, live longer and live at higher density than rural populations (Partecke et al., 2006). Ecological opportunities created by living in proximity to humans might have led to the evolution of man's best friend, but it likely created situations of increased human-wildlife conflict. This is especially the case for larger predatory species like wolves or coyotes that have the potential to attack people or pets (Poessel et al., 2013). Therefore, understanding the role of adaptation in driving behavioural changes toward humans is particularly important for developing strategies to protect the public and wildlife.

The core prediction of the dog SDH is that a wild canid population living in areas with higher human population densities will experience selection for approach (and against fearful flight responses) to human artefacts, noises and spaces (Hare & Tomasello, 2005; Hare & Woods, 2013). Secondarily, with selection for approach, it is predicted incidental traits associated with the early stages of domestication will begin to appear (i.e., morphological traits like a white tail tip, white feet, piebald spotting, white chest patch, variation in eye colour, short or curled tails, without selecting acting on these traits (Trut, 1999; Wilkins et al., 2014; Hare, 2017; Negro et al., 2017). The proposed mechanism for the appearance of these traits in domesticated species is that genetic changes expanding certain developmental periods is responsible for tamer individuals and incidentally results in developmental morphological changes alongside (Dugatkin & Trut, 2017; Hare, 2017).

Coyotes (*Canis latrans*) provide a powerful test of this core prediction as they are now established even in some of the most densely human populated areas (Weckel et al., 2015), with no obvious differences in their abundance between suburban, rural, and wild landscapes (Parsons et al., 2018). Across their range, coyotes living in areas with fewer humans experience their highest mortality from hunters and trappers, while animals living in urban areas where hunting is not permitted typically die from collisions with cars or poisoning (Collins & Kays, 2011). In addition to less risk from hunters, urban coyotes are known to benefit from more abundant prey (Parsons et al., 2018) and directly feeding on human subsidies in cities (Newsome et al., 2015).

Breck et al. (2019) provide evidence consistent with the first prediction of the SDH. Western coyotes in suburban Colorado were bolder than those in rural Utah, being more likely to approach a baited novel object, and less likely to flee when approached by people. Here we extend that work by examining the response of eastern coyotes to an unbaited novel object across

the entire state of North Carolina, including a large range of human settlement from wild to suburban. We predicted that coyotes living in areas with higher human densities would approach the novel object more, while animals in rural or wild areas would be more likely to react fearfully after noticing the novel object. We also noted the physical appearance of these coyotes, and collected other examples of unusual morphological traits in coyotes that could be associated with initial changes during selection for approach toward humans.

2. Material and methods

2.1. Apparatus and setup

We used motion sensitive camera traps to observe the behaviour of coyotes in the wild. We worked with camera trap data collected by citizen scientists, coming from 350 cameras set across 57 counties in North Carolina, across a wide range of development, on public and private lands. These cameras were set on public or private land across the state of North Carolina by citizen scientists as part of the Candid Critters project from 2017–2018. We used two brands of camera traps (Reconyx and Bushnell) that are similar in having a motion sensor, quick ($<1/2$ s) trigger times and record a sequence consecutive images in quick succession for as long as the animal was in view, illuminating with an infrared flash at night. Photographs were grouped into sequences if they were <1 min apart, identified to species, and managed by the eMammal photo management system (McShea et al., 2016), where we accessed the coyote pictures to code their behaviour.

2.2. Behavioural scoring

We used the sequences of photographs to evaluate the response of the coyote to the camera trap, thus using the camera trap both as data recorder and as the ‘novel object’ in a behavioural test of boldness (Kalan et al., 2019). In all camera trap sequences the coder was blind to housing density, average forest cover, and hunting presence. All pictures were evaluated by the same coder to ensure comparability between all traps. To avoid sampling the same individual twice, we only scored the first coyote to visit a camera trap and only used cameras spaced greater than a typical coyote home range diameter apart: 3.8 km for urban and suburban coyotes and 6.7 km diameter for coyotes living in ‘natural’ environments (Šálek et al., 2014). The exceptions to this

rule were two coyotes that had unique coloration, two pairs of sites that were 3–4 km apart but separated by a major interstate, and three pairs of coyote detections that were physically nearby but >70 days apart.

In sequences with multiple coyotes present in a group, the behaviour of each coyote was coded. The number of coyotes in a given sequence was estimated as how many individuals ran through the frame of view. Our first behavioural code was whether the coyote obviously noticed the camera, which we recognized if they made clear, direct eye contact with the camera in at least one frame; turned their head in the exact direction of the camera with no other change in body position or posture; maintained eye contact for multiple consecutive frames; showed a startle response in the frame immediately after looking in the direction of the camera; or met any of the approach criteria (see Appendix). For coyotes that noticed the camera, we classified their behaviour as an approach to the camera (a bold behaviour) if they met at least one of the following: moved in the direction of the camera while continuing to meet the notice criteria; moved in the exact direction of the camera immediately after meeting the notice criteria; sniffed or looked into the camera from an extremely short distance away; or significantly reduced the distance between the subject and camera (from distant to very near) even if a notice criteria is not met with certainty (though a notice is then coded in this case as well). If the coyote was on a trail, approaches were counted only if the coyote changed course in the direction of camera. If a coyote simply continued along a trail, even if the trail went towards the camera, it was not counted as an approach. We classified behaviour as a flee if the coyote looked directly at camera then immediately ran away until out of view. If the animal continued its motion away from the camera in a casual way, or was startled but did not immediately run out of view, it was not considered a flee. Animals that noticed the camera but did not meet the criteria for an approach or flee were classified as having ignored the camera trap. Twenty percent of notices were coded for reliability by a second coder who was also blind to housing density data and hypotheses being tested. Interobserver agreement was 90% for approaches with a Cohen's κ of 0.80 and 90% for flees with a Cohen's κ of 0.61.

2.3. Physical traits

In sequences where coyote coat colours were visible we recorded all instances of unusual colouration and type.

2.4. Analysis

Our primary hypothesis concerns coyote behaviour related to human abundance, so we quantified housing density (Hammer et al., 2004) as an average across a 5-km radius around each camera trap, matching the spatial scale of typical home range sizes for coyotes. To evaluate whether local level habitat factors affected coyote behaviour we also quantified the percentage of tree cover within a 100-m buffer of the camera trap (Hansen et al., 2013). To evaluate the potential for fine-scale response of coyotes to the local hunting risk we used local information from the camera trapper as to whether hunting was allowed on that property. We used a logistic regression and AIC model selection (Wagenmakers & Farrell, 2004) to evaluate the likelihood of approach and flee for coyotes who noticed the camera with covariates forest cover, housing density, and local hunting regulations as predictor variables. The fleeing variable was binary and coded as either present or absent in each sequence. Our approach variable was also binary and coded as either presence or absence (i.e., flees and ignores were combined into the absence category). This provided us with a simple and clear measure of whether an individual coyote responded to a novel object by fleeing or approaching.

3. Results

We scored the behaviour of 636 coyotes recorded by camera traps in 578 sequences recorded at 575 locations across 67 counties in North Carolina from June 2017–June 2019. Most (91%) were solitary coyotes, while 8% were in pairs and 1% of detections were trios of coyotes. The sequences were blurry or too short to evaluate coyote behaviour in 50 cases, of the remaining 586 coyotes, 79.9% did not obviously notice the camera trap while 118 apparently did. To avoid sampling the same animal twice, we excluded 19 of these that were close enough to be in the same coyote's home range and less than 70 days apart. Of these 99 independent coyotes that noticed the camera trap, 46 animals (46.5%) ignored the camera, 44 (44.4%) approached the camera, and 9 (9.1%) immediately fled.

None of our models predicting the flee behaviour of coyotes were significant, likely due to their relatively infrequent occurrence, but our landscape variables did predict the likelihood of a coyote approaching a camera (as opposed to not approaching, including both ignore and flee). Level of human

Table 1.

Results of logistic regression model selection testing for effects of regional urban development (ln housing density within 5 km), tree cover (within 100 m), and rather or not hunting was allowed at a site.

Model	AIC	Δ AIC	<i>p</i>	R^2
Development	132.18	0	0.0048	0.059
Development + hunting	132.30	0.12	0.0068	0.073
Development + tree cover + hunting	132.41	0.23	0.0073	0.088
Development + tree cover	132.49	0.31	0.0075	0.072
Tree cover + hunting	132.95	0.77	0.0094	0.069
Hunting	134.12	1.94	0.014	0.044
Tree cover	136.58	4.4	0.059	0.026

AIC, Akaike information criterion.

development was the strongest predictor, being the sole variable in the highest ranked model (based on AIC), and being present in all of the top four models (Table 1). Increased housing density had a positive relationship with probability of approaching (Figure 1A). Categorizing the housing densities into typical development zones (Hammer et al., 2004) shows that coyotes in suburban and exurban areas approached the camera more than those in rural areas (Figure 1B).

Seven of the 636 coyotes we examined had unusual coloration: one black, three light coloured, two with brindled coloration, and one with a white tail tip. This is likely an underestimate as some colour variants would be hard to distinguish in night-time black and white photos. These animals came from five different counties across the state. The small sample size and widespread nature of these records precluded formal analysis, although there was no obvious tendency for them to occur in developed areas. As a broader sample of unusual physical traits seen in coyotes across their range, we collected additional examples from the literature and other studies (Figure 2). These include a variety of traits known to be selected for by domestication including dog-like coat colours, white tail tips, white feet, blue eyes, shortened tails, and white chest patches. These traits were too rare to be used in a landscape analysis, are simply here to suggest the possibility of future research being designed with the intent of better understanding the presence and distribution of such morphological traits.

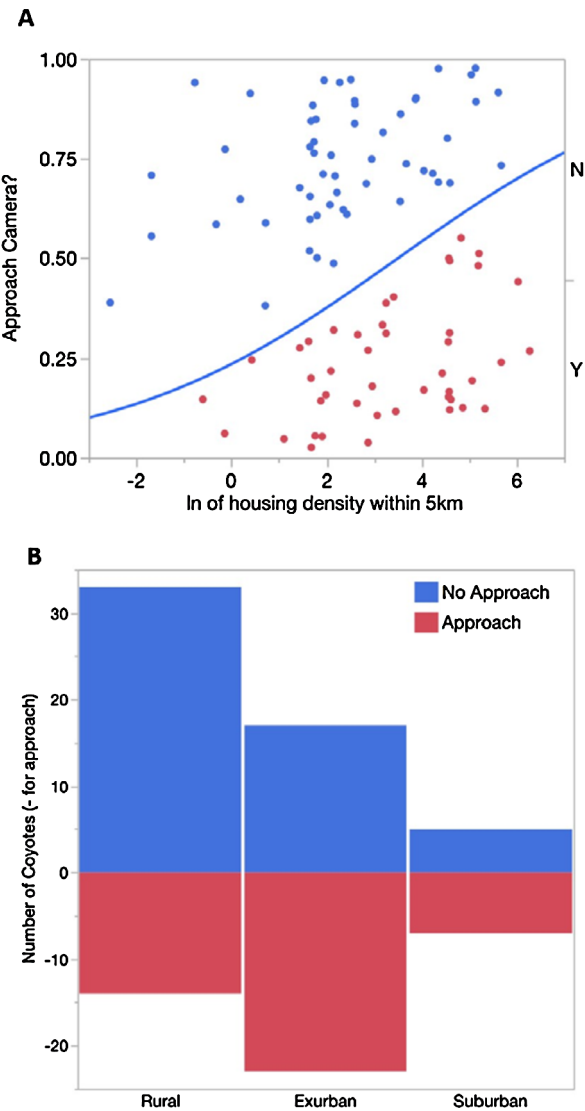


Figure 1. (A) Logistic plot showing the relationship between development level (indexed with housing density) and the probability that a coyote approaches a camera trap (red) or not (blue). (B) Bar plots show the same data with development levels broken into three commonly used categories (Hammer et al., 2004).

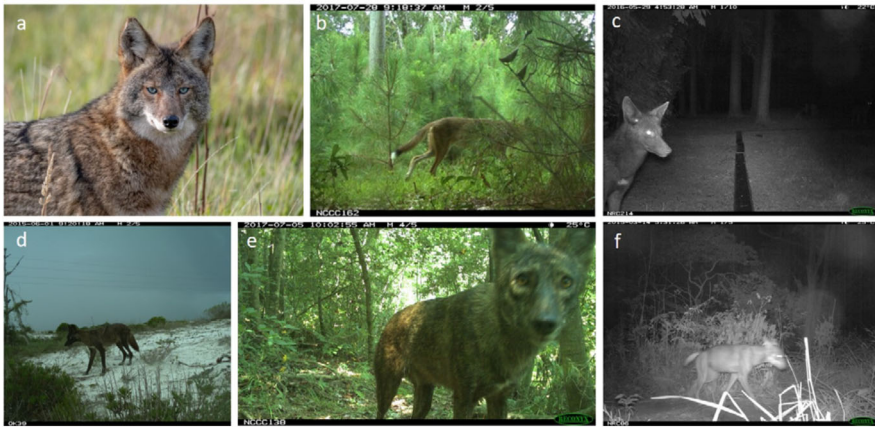


Figure 2. Predicted ‘domestication traits’ seen in wild coyotes. (a) Blue eyes, (b) white tail tip, (c) white chest patch, (d) white feet, (e) dog-like coloration (with white chest patch), (f) short tail. In the case of shortened tail it is impossible to rule out previous injury, although this was seen in three animals in different places in Panama (Hody & Kays, 2018). Credit to Brad Hyland for blue-eyed coyote picture.

4. Discussion

We found that wild coyotes’ likelihood of approaching a camera trap increased significantly with housing density (Figure 1). These results cannot be explained simply through repeated encounters with the same coyotes, as we used only the first sighting of a coyote for each trap and used only traps separated by either a major dispersal barrier (e.g., interstate highway) or a full average coyote home range diameter (according to the urbanization level, see (Šálek et al., 2014)). This result is consistent with those coyotes living in high density areas experiencing differential selection on temperament, favouring bolder individuals, as predicted by the self-domestication hypothesis. Results also corroborate similar findings in western coyotes (Breck et al., 2019) and suggests this might be a general trend for coyotes across the United States. Although in a preliminary way, we also highlight a number of cases of morphological traits in wild coyotes that are associated with the initial stages of domestication in other species. This morphological survey is far too limited to assess whether these unusual physical traits are associated with landscape or behavioural factors. While we cannot draw any conclusions here, we hope by explicitly reporting the presence of such traits in wild coyotes here, it will spur future research (i.e., via systematic examination of road kill, more high resolution trap cameras, etc.).

While we found coyotes are bolder near urban areas than those in wild and rural areas, both ontogenetic and genetic factors likely shape a coyotes' willingness to approach human artefacts. Young et al. (2019) found that coyotes can socially learn neophobic behaviours while genes under positive selection have been linked to bolder exploratory behaviour in eastern coyotes (Heppenheimer et al., 2018). This selection may be the result of higher mortality in bolder animals in rural than urban areas since hunting is not allowed in urban areas (Collins & Kays, 2011). However, gene flow may also play a role in explaining some cases of population differences in behaviour. Urban coyote populations are particularly vulnerable to genetic drift due to reduced geneflow (e.g., NYC coyotes (Decandia et al., 2019)). The pattern observed in the present work is unlikely to be explained by drift since it was observed across the state of North Carolina, not just one city (a similar pattern was also recently documented in Colorado; Breck et al., 2019). Future work can be designed to distinguish between the influence of these different factors using genetic surveys, paired with morphological and additional behavioural assays. This will allow for the identification of traits that covary as the SDH predicts, and which are shaped by other evolutionary or ontogenetic forces.

Our citizen science approach allowed for a large sample of cameras to be deployed to measure coyote behaviour across a wide range of habitats. This method did create challenges including coding behaviours from photo series as opposed to video and an inability to identify individual coyotes. We were able to compensate for the inability to identify coyotes by using camera trap sequences that were restricted to the first sequence per trap and separated in space by an average coyote home range diameter. This minimized the likelihood of recording the same individual twice. Camera traps are a common tool for scientists and hunters, so it is possible that animals in our study had seen a camera trap before our experiment. Nonetheless, the placement of our cameras was novel, in that there had not been a camera trap at this site before. Thus, the new presence of a human artefact at this location remains a useful novel object test (as recently established for chimpanzees; Kalan et al., 2019). Further, the willingness of suburban and exurban coyotes to approach the cameras represents an active, curious, approach behaviour rather than passive habituation to their presence.

While bolder approach behaviour and our preliminary collection of morphological examples are consistent with the SDH, it is also possible that

these traits originate from dog genetic introgression into coyotes. Recent research has shown that adaptive wolf (*Canis lupus*) genes for larger body size have introgressed into the eastern coyote population (vonHoldt et al., 2016). Coyotes are also known to hybridize with dogs (vonHoldt et al., 2011), so it is unclear if the behavioural and physical trademarks of domestication that we note are newly derived coyote traits or were acquired through hybridization with dogs. However, the presence of some of these dog-like traits (i.e., eye color; Figure 2) in Western coyote populations, where introgression has not been observed, suggests hybridization may not provide a full explanation. Future genomic research may distinguish between modern selection and recent hybridization with dogs, as done for black coat colour in wolves (Anderson et al., 2009). Analysis of roadkill and museum specimens across habitat types, as well as comparisons with behaviour in existing variation in captive populations, could test the relationship between morphology and behaviour more clearly and provide a strong test of key predictions of the SDH. Continued sampling over time may also reveal an increasing frequency of morphological traits associated with domestication, while more evaluations of coyote boldness in other sites could establish how widespread this phenomenon is, and whether it affects their relationships with humans.

Increasing boldness in coyotes will likely increase the potential for human-wildlife conflict. Wildlife managers often consider problem behaviours in coyotes as a progression in boldness. This starts with coyotes being seen regularly near people and escalates with attacks on pets, and then potentially, even attacks on people (Baker & Timm, 1998; White & Gehrt, 2009). Our results, and recent work by Breck et al., (2019), suggest that this boldness that leads to human directed aggression might be measurable through a novel object test, although more validation is still needed. More difficult will be determining the degree to which an increased willingness to approach humans is driven by selection on genetically inherited variation (Saetre et al., 2006) or is a case of cognitive plasticity shaped by social learning (Baker et al., 2011; MacLean et al., 2014; Schell et al., 2018). If high-risk genetic markers are established, managers could remove animals carrying them, while social learning would require research into experiences that might create more fear toward people in future generations. As coyotes continue to become increasingly successful, the well-being of both wildlife and humans will depend on pursuing the answers to such questions.

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Appendix

A.1. Supplementary guide to coyote approach coding

For each sequence:

Number of coyotes: the group size of coyotes estimated as how many individuals run through the frame of view

Number that notice: the number of coyotes that in at least one photograph of the given sequence that obviously noticed the camera because:

- Made making clear, direct eye contact with the camera,
- turned their head in the exact direction of the camera with no other change in body position or posture,
- maintained eye contact for multiple consecutive frames,
- showed a startle response in the frame immediately after looking in the direction of the camera,
- or met any of the approach criteria.

Number of approaches: the number of coyotes that

- moved even slightly in the directions of the camera while maintaining a clear notice,
- moved in the exact direction of the camera immediately after a notice,
- sniffed or looked into the camera from an extremely short distance away,
- or significantly reduced the distance between the subject and camera (from distant to very near) even if a notice criteria is not met with certainty (though a notice is then coded in this case as well).
- If the coyote was on a trail, approaches are counted only if the coyote changes course in the direction of camera (continuing along the same trail, even towards the camera, does not count)

Flee:

- animal looks directly at camera, then immediately runs away in a startled way till out of view.
- If the animal continues its motion away from the camera in a casual way it's not a freak out flee.

- If the animal is startled upon first noticing the camera but doesn't immediately run out of view it's not a flee

A.2. Examples

A.2.1. Notice

d22612s2-although the photo of the coyote looking at the camera is not completely unambiguous, the coyote reoriented itself directly towards the camera with no other change in position, meeting the criteria of a notice



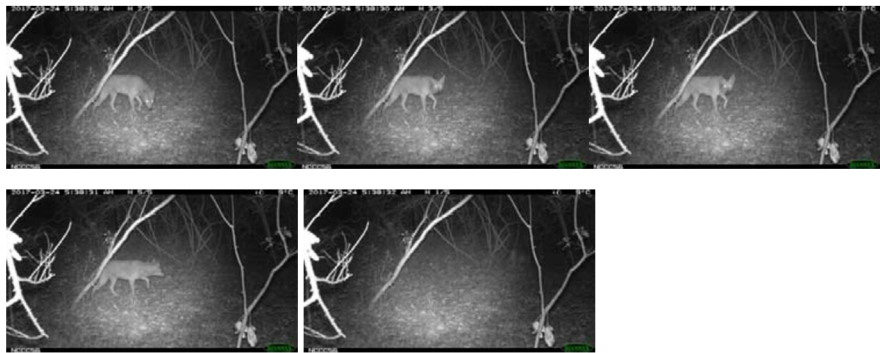
d23400s12-meets several definitions of notice, including one clear direct shot of eye contact at the camera, maintaining eye contact for multiple frames, and body adjustment that only changes to orient exactly towards the camera



d22713s7-coyote maintains eye contact for multiple frames, and eye contact in each would count as clear and direct



d22874s3-in two consecutive frames the coyote is making clear direct eye contact with the camera, so it meets the notice criteria.



A.2.2. No notice

d22936s9-the coyote may have been looking at the camera in one frame but it was too blurry to say for sure and did not last multiple frames, meaning it does not meet the notice criteria



d23127s6-although the one coyote in a blurry shot may have been looking at the camera, and the behaviour may have been a reaction to it, no images meet the criteria for a notice, so it is not counted

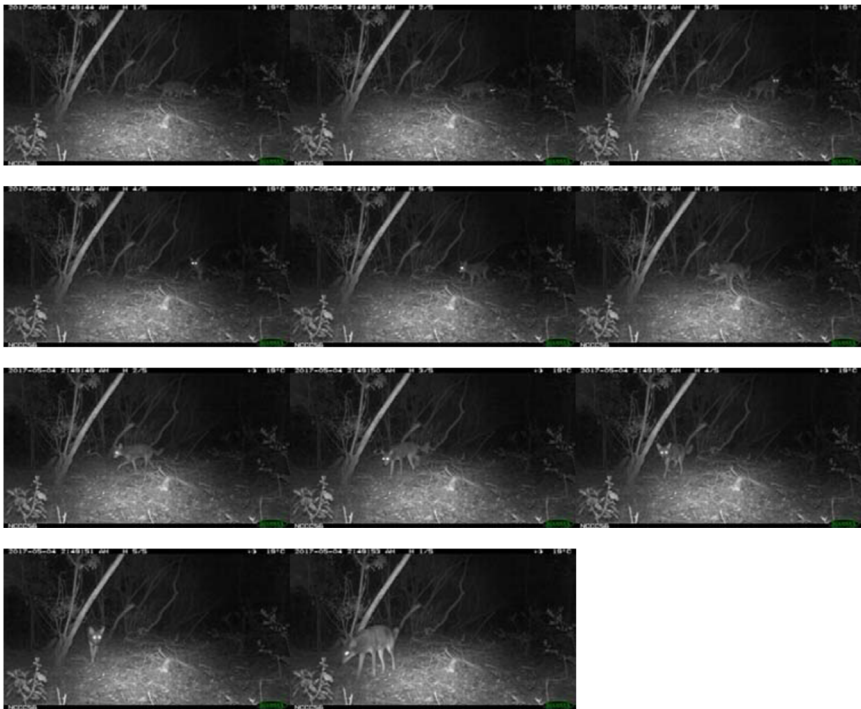


A.2.3. Approach

d22909s3-clearly moves in the exact direction of the camera while also maintain eye contact, and significantly reduced its distance to the camera, meeting several criteria for an approach



d23370s10-while maintaining eye contact with the camera, the coyote steps forward, meeting approach criteria



d22539s3-coyote moves in exact direction of camera after noticing, moves towards camera while maintaining eye contact, and significantly reduces distance to camera



d23167s1-although the coyote eventually moves away from the camera, it first steps forward while maintaining eye contact, meaning its initial reaction was approach and it meets the criteria



d22894s6-the coyote is largely out of site, but because immediately after the initial notice the coyote moves in the direction of the camera, it counts as an approach

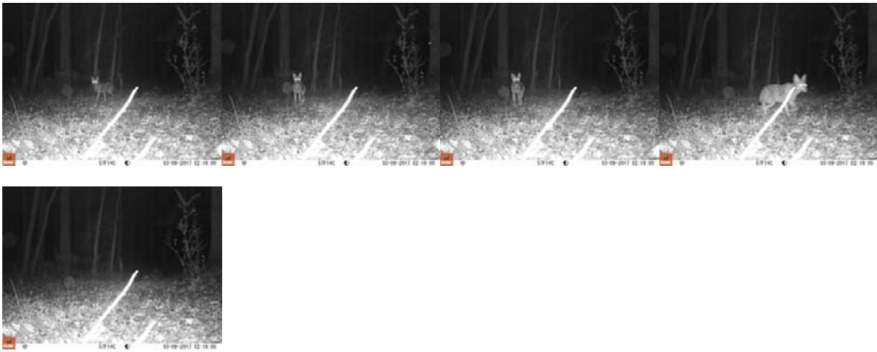


d27063s7-the first coyote initially moves toward the camera while maintaining eye contact, counting as an approach, the second coyote does not meet any of the approach criteria as described



No approach:

d22534s13-although the coyote moved vaguely toward the camera after noticing it did not significantly reduce the distance between itself and the camera, did not move forward while maintaining eye contact, and did not move exactly in the direction of the camera, meaning it did not meet approach criteria



d22562s12-although the coyote passes very close to the camera it does not obviously sniff or look into it while there, meaning it does not meet approach criteria. If in these frames the coyote looked into the camera from that same distance away it would count as an approach



d23400s12-although the coyote looks into the camera at a close distance, this is far enough away to not count as an approach, and there appeared to be no movement toward the camera after noticing it



d27668s23-the coyote notices the camera, and although it gets slightly closer to the camera while looking, it does not move directly toward the camera, does not significantly reduce its distance toward the camera, nor get extremely close to the camera, so it does not meet any approach criteria



Flee:
d27726s8-immediately after the coyote noticed the camera it ran out of the shot, with clear startle response



d43678s2-immedaitely after notice runs startled out of frame



d37155s5-immediately after looking at frame showed startle response, counting as notice, and with startle response runs out of frame, counting as flee



No flee:

d37895s1-leaves frame immediately after notice, changing direction, but with no startle response



d32210s27-after notice there is no startle response, although sequence ends before seeing clear leaving, no continued shots meaning it must have left, but no evidence of flee criteria

