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BEHAVIORAL ECOLOGY–ORIGINAL RESEARCH

Costs of territoriality: a review of hypotheses, meta-analysis, and field study

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Abstract

The evolution of territoriality reflects the balance between the benefit and cost of monopolising a resource. While the benefit of territoriality is generally intuitive (improved access to resources), our understanding of its cost is less clear. This paper combines: 1. a review of hypotheses and meta-analytic benchmarking of costs across diverse taxa; and 2. a new empirical test of hypotheses using a longitudinal study of free-living male territorial lizards. The cost of territoriality was best described as a culmination of multiple factors, but especially costs resulting from the time required to maintain a territory (identified by the meta-analysis) or those exacerbated by a territory that is large in size (identified by the empirical test). The meta-analysis showed that physiological costs such as energetic expenditure or stress were largely negligible in impact on territory holders. Species that used territories to monopolise access to mates appeared to incur the greatest costs, whereas those defending food resources experienced the least. The single largest gap in our current understanding revealed by the literature review is the potential cost associated with increased predation. There is also a clear need for multiple costs to be evaluated concurrently in a single species. The empirical component of this study showcases a powerful analytical framework for evaluating a range of hypotheses using correlational data obtained in the field. More broadly, this paper highlights key factors that should be considered in any investigation that attempts to account for the evolutionary origin or ecological variation in territorial behaviour within and between species.

Keywords Aggressive defence · *Anolis gundlachi* · Dear enemy · Nasty neighbour · Resource holding potential

Introduction

Many animal species are territorial and actively defend exclusive space or access to other resources critical for reproduction and survival. In many cases, territoriality is centred on males competing to establish or maintain a territory that overlaps the home ranges of females (or a group of females), with the benefit being better (if not exclusive) mating opportunities with those females. Territories can also provide refuges from predators and environmental conditions, as well as access to food or other ecological resources that convey fitness benefits through improved survival. Territoriality is therefore not limited to just males, but can also be found in juveniles (e.g., Stamps and Tanaka 1981), adult females (e.g., Schradin et al. 2010), and among groups of individuals (e.g., Rich et al. 2012). Territoriality is expected to evolve when fitness is linked to resource acquisition, where those resources are limited and defendable, and where there is strong competition for those resources (e.g., Kokko et al. 2006; Port et al. 2017). Conversely, territoriality can breakdown when those resources become clumped in space or time (Stamps 1983; or otherwise become abundant: sensu Keeley 2000), because the benefits of attempting to maintain exclusive access to resources are outweighed by the costs of territorial defence. Identifying these costs is consequently central to understanding why some individuals might defend territories in a population, whereas others do not, as well as how territoriality evolves more broadly.

One obvious cost from defending a territory is injury. Any dispute over resources has the potential to escalate to physical combat, where there is the risk of injury and its debilitating impact on an individual's subsequent ability to

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maintain a territory (if not on its survival as well). Yet, animals generally avoid physical combat and only do so when signal strategies are unable to resolve asymmetries in potential fighting ability. These signals are often dynamic, complex, and energetically expensive, conveying information on immediate physical condition and motivation (Clutton-Brock and Albon 1979; Waas 1991; McGregor et al. 1992; Ord et al. 2001; Moretz and Morris 2006), but they can also be simple longer term cues obtained from morphology such as weapon size (e.g., antlers, horns or other structures: Barrette and Vandal 1990; O'Brien et al. 2017) or body size. Body size in particular seems to be an important cue used by many territorial animals, with numerous studies across diverse taxa reporting physical confrontations only being likely when rivals are evenly matched in size. Costs resulting from injury are therefore unlikely to be frequent for most territorial animals simply because the resolution of most territory disputes will not require physical combat.

However, there are a number of other potential costs, and a typical territory holder can be reasonably expected to incur a combination of these costs, such as the energy expenditure required for maintaining territory boundaries through patrols or advertisement signalling, the time this maintenance takes away from other activities like foraging, and increased exposure to potential predation (see Table 1). Empirical studies typically examine just one type of cost (identified by the current study), so it remains unclear which cost(s) are especially important or common across diverse taxa. Certainly, no study has attempted to tease out the relative impact of a range of putative costs experienced by territorial animals in the wild (identified by the current study). This is a problem for our general understanding of the ecology and evolution of territoriality, because theoretical models often depend on understanding the balance between the benefits and costs associated with being territorial (Kokko et al. 2006). We know much about the benefits conveyed to territory holders from monopolising resources, especially in the context of access to mates, and we do know something about the different types of costs that might result from defending a territory (e.g., see Table 1). However, we know little about the relative impact of those different costs and subsequently which are likely to be important for most animals. Is the

Table 1 Hypotheses of the direct costs of territoriality empirically examined by past studies

Hypothesis of direct cost	Primary currency	Term of impact
Patrolling effort*		
Territories need to be actively maintained in order to preserve resource monopolisation. This maintenance will often take the form of patrolling effort, and this effort will potentially increase with the area covered by a territory. Patrols require time, energy to move, and could increase exposure to predators or adverse environmental conditions	Time, energy, condition, mortality	Immediate
Advertising ownership*		
Many animals spend considerable time broadcasting territorial ownership using signals that are often dynamic and physically strenuous. These can include vocalisations or visual displays that advertise an owner's continued presence on a territory while also conveying cues on that individual's potential fighting ability. Such conspicuous signalling is also expected to incur the additional cost of increased exposure to predation	Time, energy, condition, mortality	Immediate
Physical defence		
In addition to the risk of injury, aggressive confrontations with territorial intruders and the physical act of defending a territory through the production of directed threat signals are physiologically stressful and expected to be energetically expensive	Injury, stress, energy, condition	Immediate
Risk of predation		
Any conspicuous behaviour associated with maintaining a territory increases the likelihood of predation (or parasitism), such that individuals advertising or defending larger territories (or any territory) experience a greater chance of predation than those on smaller territories (or not defending a territory)	Mortality	Immediate
Time away from other activities		
Maintaining a territory requires the holder to physically reside on the territory, spend time monitoring territorial neighbours, and deal with intruders, in addition to any time spent patrolling and performing territorial broadcasts. Maintaining a territory subsequently diverts time away from other activities such as foraging and mating	Time	Moderate

Hypotheses are not mutually exclusive and in many cases overlap in concept. Several are also likely to contribute to the cost of holding a territory for any given individual animal. Primary 'currency' reflects some of the main forms by which costs are likely incurred and include energy expenditure, body condition, time away from other activities (e.g., that impact feeding and growth rates), physical injury, physiological stress, and increased exposure to predators or adverse environmental conditions leading to mortality. Each hypothesis is loosely categorised by the period over which impacts might be expected to manifest (immediate term, moderate term, and long term). Those asterisked were tested directly in the empirical study of territorial anole lizards (Tables 3 and 4) energetic expenditure of physically maintaining a territory a greater cost compared to the time that is diverted away from other activities? Is there a difference between long-term versus short-term costs, such as the impacts on growth rate versus the day-to-day physiological stress that might be experienced in dealing with frequent territorial intrusions? Is the type of resource monopolised by defending a territory (e.g., mates, nest sites, refuges, or food) linked to the magnitude of costs suffered by territorial holders?

Even for some better-studied territorial costs, there is often conflicting evidence over whether those costs actually occur for a given system. For example, maintaining a territory is widely assumed to be so costly to territory holders that they suffer reduced survival or body condition, but some studies document no relation to survival (e.g., Munguia-Steyer et al. 2010) or a positive (not negative) association between holding a territory and a male's condition (e.g., Aluja et al. 2008; Peixoto and Benson 2008, 2011). This is presumably because males in better condition are more likely to successfully compete for a territory or have obtained the benefits of any monopolised food resources that might be available on a territory. Individuals without a territory have also been shown to exhibit higher physiological stress and poorer body condition than those occupying a territory (Young and Monfort 2009). A number of classic studies report how territorial males expand their territories when experimentally supplemented with food. This is consistent with the notion that physical condition (improved here by supplemented food) has a positive effect for defending a larger territory (Arvidsson et al. 1997). However, even in this specific context, the data are not clear. A qualitative review of food supplement experiments found the majority of studies reported territories shrink with increasing food resources or that food supplementation had no effect at all (Adams 2001). The point being, even for the most popular assumptions on how costly territoriality might be, the data are often conflicting, and if hypotheses are correct, the underlying mechanisms are clearly not straightforward.

The objective of the current study was to identify the costs that might be associated with being territorial and to quantify the relative contribution of those costs to help resolve which were likely to be relevant for most animals. In the process of reviewing the literature, it became clear that empirical investigations were almost always limited to a single cost (Table 1) or at best an exacerbating factor that might indirectly impact several costs associated with maintaining a territory (Table 2). A second objective was therefore to illustrate an analytical approach that can be easily implemented using field-collected data and used to test various hypotheses concurrently to reveal how different factors are related to one another. The study therefore had two components: (i) a review and subsequent meta-analysis of representative past studies that examined some aspect of the cost of being territorial, and (ii) a longitudinal study of free-ranging territorial lizards that tested several hypotheses identified by the review, in addition to two new hypotheses not previously considered.

For the review and meta-analysis, the primary goal was to identify the range of hypotheses that previous studies have considered in their empirical investigations of territorial costs, and then benchmark those findings using meta-analytic approaches to gauge their relative biological effect. This review highlighted nine hypotheses that have been explicitly or implicitly tested (Tables 1, 2). Most of these hypotheses were centred on the impact of defending a territory in relation to the direct costs of energy expenditure, time away from other activities, and physiological stress. Other hypotheses considered factors that were better described as exacerbators of direct costs, such as the length of time on territories or the nature of the competitive environment experienced by territory holders. I also present two additional hypotheses (Table 2) partly inspired by the natural history of the lizard species used in the empirical component of the investigation (outlined below), but should nevertheless be broadly applicable to other territorial animals. These hypotheses were centred on the exacerbating impacts of the environmental conditions experienced by territorial holders that lead to difficulties in effectively advertising territory ownership (e.g., Ord et al. 2016) and monitoring territorial intrusions (Ord and Stamps 2008), and the sensitivity of ectotherms to ambient temperature and its impacts on activities like patrolling and advertisement display (e.g., Ord and Stamps 2017; see Table 2 for details).

For the longitudinal empirical study, I leveraged field-collected data for a Puerto Rican species of anole lizard where male territorial holders had been repeatedly observed several times a day over many weeks (Ord et al. 2016). These data were evaluated using various statistical models that corresponded to different hypothesized costs and exacerbating factors uncovered by the literature review (Tables 1, 2). This included a flexible form of path analysis (Shipley 2013) that enabled exploration of the potential interaction of putative casual factors. The model selection approach applied was especially suited to field-collected data that are often limited by sample size. It therefore allowed a statistically powerful test of multiple hypotheses to be made concurrently, while also providing a means of identifying the potential presence of unmeasured costs, which can then be the subject of follow-up study.

The lizards used in this empirical investigation belonged to a population of *Anolis gundlachi* living in the deep-shade forest of the Luquillo Mountains on Puerto Rico. Male lizards of this diurnal, arboreal species aggressively defend territories that encompass several trees and the home ranges of several resident females. Territories also provide other resources including refuges and food (e.g., Stamps 1977).

Table 2 Hypotheses of factors expected to exacerbate one or more direct costs and have been empirically examined by past studies or were new for this study

Hypothesis of cost exacerbator	Direct cost(s) impacted	Term of impact
Noisy environments (new from this study)*		
Effective broadcast signals must be conspicuous to conspecifics and this is dictated by the physical properties of the surrounding environment as well as the distance over which broadcast signals must travel to reach neighbours and other potential rivals. Territory holders in ‘noisy’ areas of the environment or maintaining large territories will have to compensate by increasing the rate of signal broadcasts or the magnitude of those broadcasts (e.g., sound volume or display exaggeration), resulting in more time spent and potentially greater energetic expenditure. Noisy environments will also impact the ability of territory holders to monitor territorial intrusions and require greater patrolling effort	Advertising ownership, time away from other activities, patrolling effort	Immediate
Temperature (new from this study)*		
Ambient temperature impacts the activity of most animals by affecting metabolic rates and subsequent energy expenditure (especially for ectotherms). Animals defending territories in cooler environments will therefore have greater difficulty in performing the physical activities needed to maintain territory (patrolling, signalling)	Patrolling effort, advertising ownership	Immediate
Competitor pressure*		
High population density or otherwise an increased pressure from rivals over territory space will result in more aggressive disputes and greater effort in maintaining an exclusive territory (e.g., frequent patrolling and territorial broadcasts)	Patrolling effort, advertising ownership	Moderate to long
Competitor familiarity		
As territory boundaries become stable in space and time, familiarity among territory neighbours will progressively reduce the need for activities associated with maintaining and defending territory boundaries (the so called “dear enemy” hypothesis). Conversely, territory holders of newly acquired territories, or long-term territory holders that experience frequent turnover in the ownership of neighbouring territories or an influx of ‘floaters’ passing through the social neighbourhood, will have to frequently patrol and defend new or previously established territory boundaries against rival intrusions	All	Moderate to long
Owning a large territory*		
Larger territories require more effort to patrol and advertise ownership, and are more prone to intrusion because of their increased boundary length and number of surrounding territory neighbours, compared to smaller territories	All	Long
Longevity on territory		
Costs associated with defending a territory progressively accumulate over time the longer a territory is maintained (the so called “nasty neighbour” hypothesis or situations in which territory owners are frequently challenged by new rivals). Residents on older territories will therefore have poorer condition or a greater likelihood of mortality compared to those on newer territories, or by the end of a breeding season compared to the start	All	Long

Hypotheses are not mutually exclusive and in many cases overlap in concept. Several are also likely to contribute to the cost of holding a territory for any given individual animal. Each hypothesis is loosely categorised by the period over which impacts might be expected to manifest (immediate term, moderate term, and long term). Those asterisked were tested directly in the empirical study of territorial anole lizards (Tables 3 and 4)

Previous study of this population has shown that male territory holders face important challenges from low light and high visual noise from windblown vegetation that reduces the conspicuousness of territorial advertisement displays (Ord et al. 2007, 2016; Ord and Stamps 2008). These displays are delivered from perches at various points inside a male’s territory and consist of a complex series of head-bob/push-up movements and the extension of a large throat fan or dewlap. Males compensate for moment-to-moment fluctuations in visual conditions—deteriorating light and increases in background visual noise—by increasing the speed and duration of head-bob/push-up movements, while adding prolonged dewlap extensions (Ord et al. 2010, 2016). Furthermore, males spend a considerable amount of time performing territorial advertisement displays—an average of one display bout every 5 min (Ord and Stamps 2017)—but this display rate is strictly, and positively, dependent on ambient temperature because of the underlying temperature dependence of physical activity in these lizards (which is apparently a direct consequence of the impact of temperature on metabolic processes: Ord and Stamps 2017).

The ten males were selected, because they occupied territories in areas of the forest that tended to differ in the viewing conditions mediated by ambient light and visual noise, and temperatures experienced over the duration of the day. Differences in ambient temperature were expected to generate differences in the amount of time males were able to spend performing territorial advertisement displays and other territory maintenance behaviours (e.g., patrolling). Alongside the two hypotheses relating to the signal environment and temperature, I also tested four hypotheses from the review (Tables 1, 2) using detailed information on patrolling effort, the rate of territorial advertisement, territory size, and the competitive environment. These hypotheses were evaluated based on changes in body condition, which was the most common direct cost measured by past studies (identified in the current study).

Materials and methods

All analyses were conducted in R version 4.0.5 (R Development Core Team, R Foundation for Statistical Computing, Vienna).

Review of empirically investigated hypotheses and associated meta-analysis

I conducted my search and screening process as outlined in the PRISMA diagram presented in Fig. S1. This was done to provide a systematic framework for my review and to facilitate identifying hypotheses of the cost of territoriality that have been empirically investigated in the past. I then took the opportunity to implement a meta-analysis as a means of quantitatively benchmarking findings from these studies, following the general guide presented by Nakagawa et al. (2017).

To conduct the review, I first conducted a search of the ISI Web of Science database across all years using a combined topic search for the keywords 'territor*' and 'expens*', and 'territor*' and 'cost*'. This uncovered 11,889 records. These were further refined to the categories 'zoology', 'ecology', 'behavioral sciences', and 'evolutionary biology' for a subtotal of 2053 records. The abstracts of all these records were examined and the 213 papers that appeared to measure some type of cost relating to territoriality or territorial aggression were downloaded for detailed review. Criteria for inclusion in the meta-analysis required that a study had measured some type of cost and compared that cost to a benchmark. Cost was considered to be any factor that could be reasonably expected to impact the health or survival of a territory holder, such as physiological stress, energy expenditure, body condition, growth, food intake, time away from foraging, injury, or mortality. Benchmarks were other same-sex individuals or within-individual measures that could be used to gauge the magnitude of a cost. For example, comparisons included territorial versus non-territorial animals, animals holding different territory sizes, animals defending territories in high versus low competition environments, a territorial holder assessed following an aggressive encounter or bout of territorial advertisement versus at rest, and a territorial holder at the end of a breeding season versus the start of the breeding season. Furthermore, it had to be possible to extract data for computing the magnitude and variance of cost differences, either from information reported in the text or from data presented in figures.

The final dataset included 42 studies, examining 41 species (12 bird, 11 mammal, 8 fish, 4 lizard, 4 insect, and 2 amphibians) and 99 comparisons. This dataset was not meant to be exhaustive. Instead, the objective was to conduct a systematic review that would avoid bias in the types of studies evaluated (which might occur when taking an ad hoc approach of qualitative review). Nevertheless, as a foundation for the meta-analysis that followed, the dataset can be expected to cover a large, representative sample of the empirical studies that have been published and, importantly, includes a diverse range of taxa and methods of cost assessment.

For the meta-analysis itself, I used the package 'compute.es' version 0.2-4 (Del Re 2013) to compute a standardised effect size and its associated variance for each cost comparison reported by a study using Hedge's *g* (see Borenstein et al. 2009 for description and formula; NB: *g* was selected simply because the majority of the studies reported findings that were most suited for computing this type of effect size). These values were then aggregated where appropriate within each study to account for non-independence of study effects using the package 'MAd' version 0.8–2.1 (Del Re and Hoyt 2014; NB: where multiple effects were compiled from a study, these were typically computed using the same benchmark group or based on measures taken from the same animals, which was best accounted for using the 'aggregate dependent effect sizes' function in MAd; see Borenstein et al. 2009 for discussion). I then used the package 'metafor' version 2.1-0 (Viechtbauer 2010) to apply a linear model to compute the final effect estimate for a given set of comparisons. I first used Akaike information criterion (AIC) to assess various estimators of heterogeneity, and in all cases, a random-effects model with a restricted maximum-likelihood estimator was found to be the best-supported model. I also considered the potential for publication bias in the data using funnel plots and trim-and-fill analyses implemented in 'metafor'. In the handful of cases where probable missing data were identified, I used the 'trimfill' function to recompute the aggregated effect size and present these alongside those computed exclusively on the available data. Finally, to provide a bounded measure of effect size that would be familiar to most readers regardless of their experience with meta-analysis techniques, I converted g and its corresponding upper and lower 95% confidence intervals (CI) into r using formulae presented in (Ord et al. 2011; see also Borenstein et al. 2009).

Field study

Intensive observations of ten adult male *A. gundlachi* territory holders were made in the forest around the El Verde Field Station on Puerto Rico. Observations were initially conducted as part of a larger study described in Ord et al. (2016) and Ord and Stamps (2017). What follows are details specific to those individual lizards and procedures used for the present study.

Male *A. gundlachi* were easily identified by their large dewlap. Initially, 26 male lizards were marked using colour-coded "bee" tags for individual identification from a distance. Many of these lizards ultimately lost their tags through moulting (7) or quickly disappeared and were likely non-resident males passing through the area (5). Of the remaining 14 lizards, four evaded capture at the end of the study and could not be included in the current study, because changes in body condition could not be evaluated. The final ten male lizards were visually isolated in different parts of the forest and separated by many intervening territories of other conspecific males.

Lizards were captured and weighed using a spring balance to the nearest first decimal gram and their snout-to-vent length (SVL) measured with a metal ruler to the closest millimeter. Each male was observed between dawn and dusk two-to-four times a day in a systematic manner that ensured lizards were observed across a full range of times each day for up to 26 days (median: 25 days; range: 10–26 days). Each observation consisted of video recording the resident male for 15 min using a camcorder on a tripod and noting each perch he displayed from, which was then flagged and numbered at the end of each observation period. During video recording, the surrounding environment was carefully surveyed for other male *A. gundlachi* to identify potential territory neighbours. Neighbours were considered to be any adult male conspecific within 10 m of the resident male (this distance corresponds to the maximum distance that *A. gundlachi* territorial displays are likely to be detected by receivers in this forest; see Ord and Stamps 2008). At the end of the observation period, a compass bearing to each male neighbour was taken and distance determined with a tape measure to the nearest centimeter from the perch on which the resident male was first observed at the start of video recording. The opportunity was also taken to measure ambient light levels at this perch using a LiCor LI-190SA Quantum Sensor attached to a handheld LI-205A light meter and ambient air temperature to the nearest decimal place using a Skymate Wind Meter. Light was averaged across observations for a given male, while temperature was similarly averaged but also summarised as range across observations.

At the end of the study, lizards were recaptured, weighed, measured for SVL (as above), and bee tags removed. Each male's territory was then surveyed using a tape measure anchored at a central tree within the male's territory (inferred from the distribution of flagged perches). From this point, a compass bearing and distance to every tree was recorded (to the nearest centimeter; as well as its diameter to the nearest millimeter) that occurred within a circumference inclusive of all marked perches used by that male during the study. These data were then used to map the position of all trees, perches, and territorial neighbours to scale using adobe illustrator software (Fig. S2 provides an example). On this diagram, all outer perches used by the male during the study were connected with a line (median number of observations per male territory holder: 59; range: 33–67) and the area enclosed by these perches was used to infer his territory size (in m^2; see Fig. S2).

Video recordings were scored manually to quantify the number of head-bob/push-up display bouts performed during each observation to compute the mean rate of territorial advertisement display (bouts/min). Clips of each bout of display were also edited from videos and the amount of visual noise generated by windblown vegetation occurring in the background was quantified using the MatLab-based program "Analysis of Image Motion" (Peters et al. 2002; see Ord et al. 2016 for details on how this software was implemented). These data were summarised as the maximum speed of motion occurring in the background of each clip, which was then averaged across displays for a given observation, and averaged again across observations to obtain a final estimate of visual noise specific to that male's territory.

The proportion of researcher visits to a particular male's territory that concluded with the male being spotted (and subsequently video recorded) was used to estimate the proportion of visits that a lizard was found occupying his territory. For example, one particular male was visited 77 times during the study and was found occupying his territory on 67 of those occasions and absent the remaining 10, for a proportion of 0.87 (a value of 1 would correspond to a lizard always being found on his territory; NB: the median number of visits across the ten male lizards was 70, with a median presence of 59 and absence of 13). A male was only noted absent once the researcher had spent 10–15 min visually searching the male's territory and failed to observe the male, following which the researcher moved on to the next male on the roster. While it was possible a male might have been present but missed during this search, extensive experience studying this species at this location suggests this would have been unlikely. Furthermore, the vegetation structure encompassed by territories varied to some extent among males, but not in a manner that would have systematically biased determination of territory holder presence. The forest at this location consisted of a high, dense canopy and open understory, such that the males were easily spotted perched on one of the various trees within their territory. Those instances where a male was recorded absent almost certainly occurred, because that male was out of sight up in the canopy or off their territories entirely. In either case, the male would not have been visible to territory neighbours. The proportion of researcher visits in which a male was found was therefore used to approximate a male's physical presence on his territory.

The total number of perches used by males ranged from 5 to 14, but this did not provide an accurate reflection of how often a male patrolled his territory. For example, a male with seven perches within his territory was typically found on the same one or two perches throughout the study, whereas another male with five perches within his territory was frequently seen using several of those perches. The total number of perches within a male's territory was also confounded by gross territory size (i.e., the total number of perches within a territory tended to be positively correlated to territory area: Pearson's correlation = 0.61, df = 8, and $p = 0.059$). Instead, the variance of the proportional use of perches was used as an index of patrolling effort. Here, the number of times a given male was observed on a particular perch was divided by the total number of times a male was observed. The variance of this proportional use was then computed across all perches, with low values corresponding to a male that was often seen using a range of different perches on his territory, while high values corresponded to a male that was often seen on the same perch time and time again. This variance in proportional perch use was also statistically independent of gross territory size (Pearson's correlation = − 0.25, df = 8, and $p = 0.48$).

Finally, to compute body condition, I first combined weight and SVL data taken for the ten males at the start of the study with data collected in an identical manner for 21 other *A. gundlachi* males at the same location retrieved from my personal data archive. I then regressed body weight (g) on SVL (mm) to compute a growth rate model for the population (this was best fit by a linear model: weight = − 6.83 + 0.22SVL, $r^2 = 0.48$; Fig. S3a). This growth rate model can be viewed as the 'on average' change in body weight expected for a given change in SVL for this population, based on the subset of males examined (31 males). It will be inclusive of both the positive and negative factors affecting the average growth rate for the average lizard in this population. I then used this equation to compute the residual value of weight on SVL for the ten male lizards at the start and end of the study and took the difference of the two values. This difference score was then divided by the number of days between the start and end measure (range: 10–26 days) to provide a final value that reflected the average daily change in body weight across the study, standardised by the inferred growth rate for lizards in this population. Males with positive values gained weight beyond what would be expected for the population average growth rate over the time they were observed (i.e., improved in condition), while those with negative values lost weight more than expected for the average growth rate over the course of the study (deteriorated in condition; NB: depending on a male's starting condition, he may still be of superior condition than other males in the population).

The statistical investigation was conducted in two parts. First, I created 11 linear models [*m*1–11] corresponding to six different hypotheses of how male condition might be impacted by territory ownership (Fig. 1; see Tables 1, 2). These models were evaluated against each other using the second-order correction of Akaike information criterion ($\mathrm{AIC_c}$). This value of $\mathrm{AIC_c}$ was then used to compute a relative level of support—or conditional probability—for given model compared to all models considered (*w*). The model with the lowest $\mathrm{AIC_c}$ value is typically considered to be the best-supported model, but any model within two $\mathrm{AIC_c}$ units of this model should be considered to be equally credible (Burnham and Anderson 2002). More specifically, those hypotheses that obtain largely equivalent levels of support ($\Delta\mathrm{AIC_c} \le 2.0$) can be considered to be complementary explanations for the data, whereas those that clearly differ in support are going to be those that, in general, are mutually exclusive or competing hypotheses. In addition to allowing alternative hypotheses to be evaluated against each other, model selection avoids the pitfalls of "significance" testing and *p* value corrections for multiple comparisons (requiring the use of false discovery rate or Bonferroni) and instead focusses interpretation on effect size estimates (*r*, *t,* or other effect statistics; Nakagawa 2004; Garamszegi 2006; Burnham et al. 2011; Symonds and Moussalli 2011).

The model sets considered either direct costs [*m*1–*m*3] or exacerbators [*m*4–*m*10] of unmeasured direct costs (represented by 'variable X_i' in Fig. 1) that assumed a progressive deterioration in body condition across males as a function of:

> Patrolling effort: [m1] increasing proportion of time each male territory holder was physically present on his territory or [m2] decreasing variance in the proportional use of different perches (corresponding to a male frequently shifting among perches on his territory).

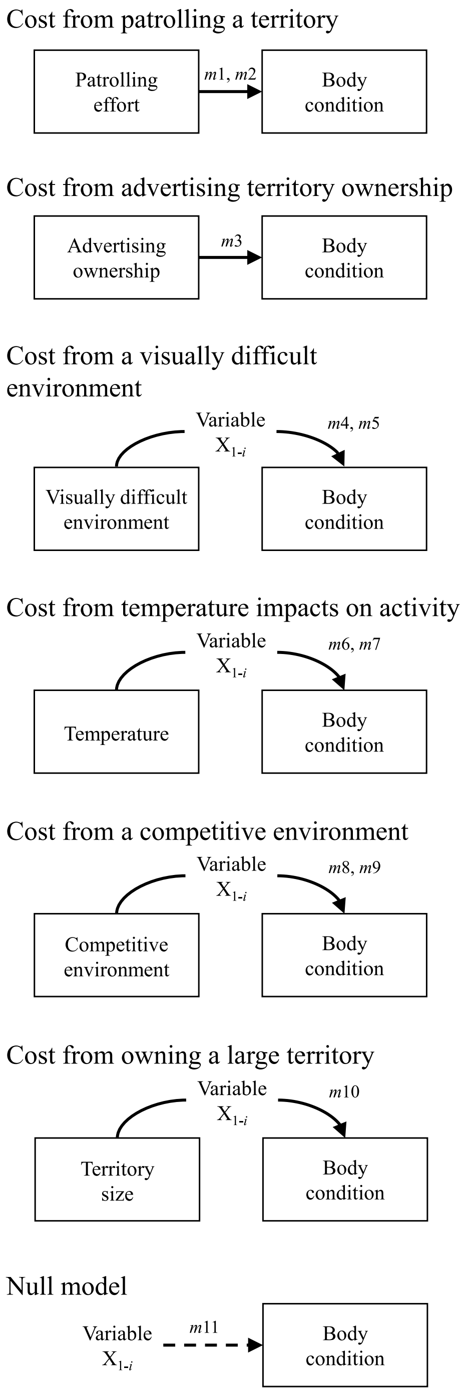

Fig. 1 Models applied in the empirical study of territorial Puerto Rican *A. gundlachi* lizards that tested the direct cost and exacerbator of costs (via an unmeasured 'variable X') associated with defending a territory

Advertising ownership: [m3] the increasing mean rate of territorial head-bob/push-up displays performed across male territory holders.

Noisy environments: [*m*4] increasing amount of visual noise or [*m*5] poor ambient light impeding the ability of territory holders to advertise ownership effectively and track potential intrusions by rivals or neighbours.

Temperature: territory holders experiencing [*m*6] low mean temperatures on their territories, or [*m*7] a wide range of fluctuating temperatures, that impacts a male's ability to actively maintain and defend his territory.

Competitive pressure: [*m*8] increasing numbers of male neighbours surrounding a territory holder, or [*m*9] decreasing distances to the closest male neighbours (with closer neighbours corresponding to greater pressure for space).

Owning a large territory: [*m*10] increasing territory area occupied across male territory holders.

These models were further benchmarked against a null (intercept-only) model [*m*11] that effectively assumed changes in body condition either varied stochastically among males or has been influenced by some other unknown factor. To illustrate the effect size of the best-supported model and any other potentially credible models, I report the correlation coefficient, *r* (converted from the r^2 value computed for the overall model), which is comparable to the meta-analysis effect sizes shown in Fig. 2.

Second, given the clear support for the model linking the size of a male's territory to his deterioration in body condition ([*m*10] see Results), various path analyses were evaluated to determine the extent to which this relationship reflected the impact of territory size on the competitive environment experienced by a territory holder and his subsequent patrolling effort and display activity. In its most complex form, this sequence might appear as follows (Fig. S4): males occupying larger territories are surrounded by more or closer territorial neighbours, which prompts greater patrolling effort by that male, and this increased energy expenditure results in a decline in body condition, compared to males maintaining smaller territories with fewer or farther rival neighbours that require less patrolling effort to enforce territory boundaries. Various paths were possible for other exacerbating factors as well (illustrated in Fig. S4), but these were not formally considered, because none of the initial models associated with those hypotheses [*m*4–*m*9] received credible support.

Path analyses were implemented using the method developed by Shipley (2013), which circumvents many of the constraining assumptions of classical path analysis, mediation analysis, or structural equation modelling (SEM). It relies on directed separation (d-separation or d-sep tests) of directed acyclic graphs (DAGs). I used the 'ggm' package version 2.5 (Marchetti et al. 2020) to first identify the basis sets of each d-separation claim in a path model and then obtained the null probability of those claims using standard linear regressions implemented in the base package of R. However, the beauty of Shipley's method is that it allows

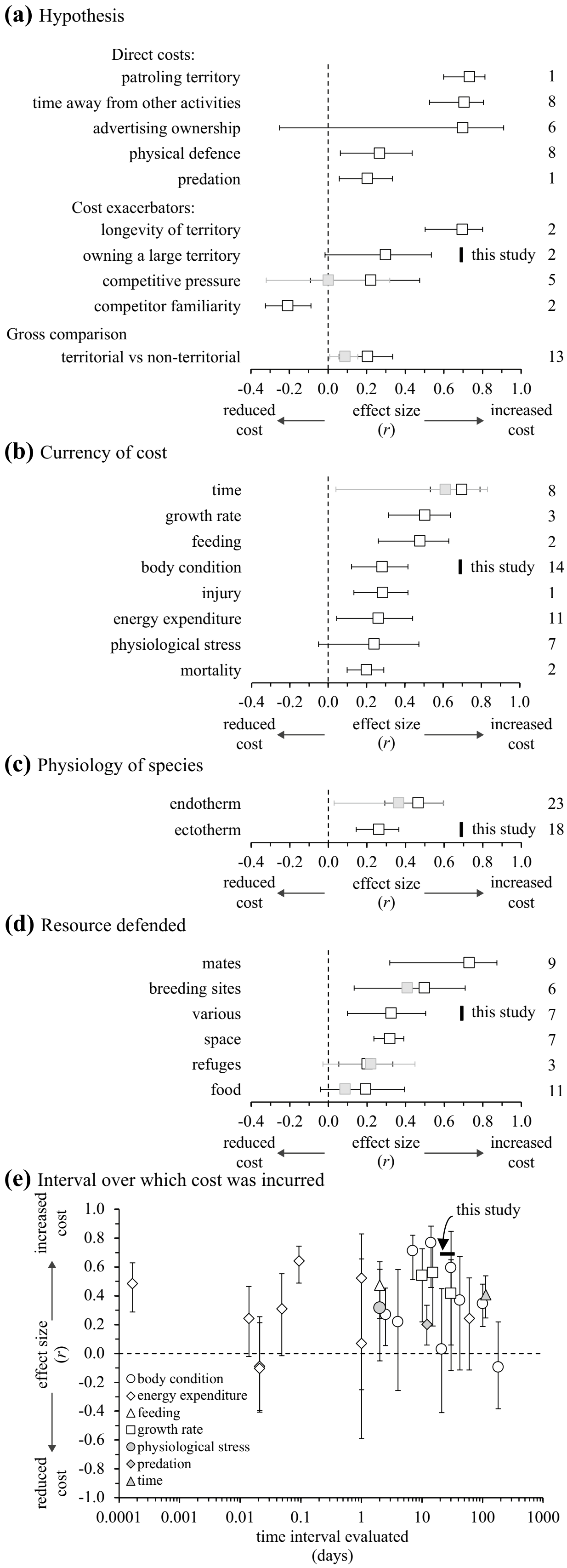

Fig. 2 Meta-analysis of findings extracted from studies used to identify hypotheses of the expected costs of being territorial (hypotheses are described in Tables 1 and 2). Data were examined in the following contexts: **a** general hypothesis of cost investigated, **b** currency of cost incurred, **c** physiology of species, **d** type of resources being monopolised by maintaining a territory, and **e** timeframe over which cost was assessed. Error bars are 95% confidence intervals. Numerals to the right of the upper 95% confidence limit in **a**–**d** are the number of studies used to compute the aggregated effect size. Shaded symbols in **a**–**d** are recalculated effect sizes that attempt to account for suspected publication bias. See Figure S5 for a breakdown of each studies computed effects and sample size. Sources consulted: Abell (2000), Amsler (2010), Ancona et al. (2010), Bachman and Widemo (1999), Baldo et al. (2015), Berger-Tal et al. (2015), Border et al. (2019), Brown and Sherry (2008), Cleveland (1999), Contreras-Garduno et al. (2006), Corlatti et al. (2013), Dias et al. (2010), Ezenwa and Snider (2016), Gordon (2004), Isvaran and Jhala (2000), Jaeger (1981), Lebigre et al. (2013), Low (2006), Maan et al. (2001), Marino (2012), Martinez-Padilla et al. (2014), McLeod and Ritchison (2018), Noel et al. (2005), Pearson et al. (2006), Praw and Grant (1999), Riebli et al. (2012), Rimbach et al. (2019), Romo-Beltran et al. (2009), Ros et al. (1997), Rusch and Angilletta (2017), Schutz et al. (2010), Siracusa et al. (2021), Takeuchi (2006), Tiebout (1993), Velde and Van Dyck (2013), Viera et al. (2011), Vollestad and Quinn (2003), von Kuerthy et al. (2015), Wikelski and Trillmich (1994), Willisch and Ingold (2007), and Young and Monfort (2009) ▶

virtually any combination of statistical models to be applied, enabling individual models to be tailored to the specific properties of the data (binomial, categorical, or continuous; normally distributed or otherwise), its hierarchical structure (e.g., inclusion of random effects), and expected relationship between variables (linear or non-linear). It also allows the comparison of different path models using AIC. This is done by combining the null probabilities of the d-separation claims into a C-statistic, which is then converted into AIC_c. A detailed description and easy to follow worked example of the method is provided in Shipley (2013). To illustrate the effect size of putative casual links among variables in each path model, I report the *t* values computed for the associated predictor slopes.

Results

Literature review and meta-analysis

Various non-mutually exclusive hypotheses have been empirically examined in past studies and these could be qualitatively summarised into nine general hypotheses outlined in Tables 1 and 2. Hypotheses were either those expected to result in direct costs to territory holders or those expected to exacerbate or magnify the impact of one or more costs. The form or 'currency' of costs varied from increased energy expenditure, time away from other activities, physiological stress, and exposure to predators or adverse environmental conditions leading to an increased risk of mortality (Table 1).

Subsequent quantitative synthesis of the data extracted from studies confirmed that the cost of territoriality was generally high for most animals (Fig. S5). Based on the general benchmarks of small ($r = 0.10$), modest (0.24), and large effects (0.37; see Cohen 1969), the aggregated effect of these costs across 41 species was large ($r_{\text{available data}} \pm 95\%$ confidence interval, CI: 0.35, 0.25–0.44), or modest if we assume underreporting (r_{trimfill}: 0.30, 0.18–0.41 with six inferred missing data) and based exclusively on a gross comparison of territorial versus non-territorial individuals within a population (Fig. 2a). Nonetheless, there was high variability in estimated cost across studies and species (Fig. S5), which to an extent could be attributed to the type of cost examined (Fig. 2a, b).

The biggest costs for territorial animals appeared to be those associated with time diverted from other activities (Fig. 2a; including feeding, see Fig. 2b) and the longevity of holding a territory more generally (Fig. 2a). Patrolling a territory was also potentially very costly, but this evidence was based on a single study in primates (i.e., Amsler 2010). The cost associated with advertising territory ownership seems to be high for many animals, but this cost was nevertheless variable and the computed 95% CIs were wide and overlapped zero. Physically defending a territory was moderately costly, as was maintaining a large territory (be it not statistically significant with a lower CI marginally overlapping zero; Fig. 2a). Competitive pressure was the least likely hypothesis to exert a cost on territory holders (Fig. 2a). Despite being relevant for a number of territorial species (see Discussion), studies on the consequences of familiarity among neighbouring territory holders in moderating defence costs (e.g. "dear enemy"; Table 2) have been rare. In the two cases where costs had been explicitly measured and could be included in the meta-analysis, the costs incurred were considerably reduced when territory holders were familiar with their neighbours, compared to situations where territory holders experienced frequent turnover in neighbours or intrusions by unfamiliar rivals.

Aside from the currency of time and reduced feeding, growth rate was commonly impacted in territorial animals, followed by body condition, which was also the most frequently measured cost outcome overall (Fig. 2b). The behaviours associated with maintaining a territory were also moderately energetically expensive, and tended to increase the likelihood of injury and mortality (Fig. 2b).

Endotherms tended to incur slightly higher costs than ectotherms, although there appeared to be some underreporting, and in any respect, the 95% CIs overlapped between the two groups (Fig. 2c). Territories that were typically used to monopolise access to mates or resources used for reproduction (nest sites, oviposition sites) were associated with the highest costs (NB: this effect does not reflect the cost of reproduction, but specifically the cost incurred from the aggressive defence of those resources). Many species were reported to defend territories that monopolised access to various resource types, and the associated costs of these territories were similarly high (Fig. 2d). In contrast, costs from the aggressive defence of refuges and food were largely negligible (Fig. 2d). There was no obvious association between the magnitude of a cost and the time interval over which that cost had been measured (Fig. 2e).

Field study

The most consistent predictor of reductions in body condition among the ten male *A. gundlachi* was the unmeasured cost(s) associated with defending a large territory (Table 3; Fig. 3a; $F_{1,8} = 7.19$, $p = 0.028$). Territory size varied almost

Table 3 Costs of territoriality tested for male territory holders of the Puerto Rican lizard *Anolis gundlachi* as measured by changes in body condition over several weeks

Hypothesis Predictors of changes in body condition	ΔAIC_c	ω	*r*
Direct costs			
Patrolling a territory			
Time on territory [*m*1]	6.4	0.02	
Perch use around territory [*m*2]	6.1	0.02	
Advertising territory ownership			
Head-bob display rate [*m*3]	5.2	0.04	
Cost exacerbators			
Difficult visual environment			
Visual noise [*m*4]	3.2	0.10	
Ambient light [*m*5]	6.3	0.02	
Temperature effects on activity			
Average temperature [*m*6]	6.3	0.02	
Range in temperature [*m*7]	3.6	0.09	
Competitive environment			
Number of male neighbour [*m*8]	5.3	0.04	
Distance to nearest male neighbour [*m*9]	5.5	0.03	
Owning a large territory			
Gross size of territory [*m*10]	0.0	0.51	0.69
Null model			
Intercept only [*m*11]	3.2	0.10	

Corresponding statistical models described in the text are reported in square parentheses

Direct costs are those that are predicted to have a principal contribution to changes in body condition, while exacerbating factors are those predicted to contribute to changes in body condition via their influence on one or more direct costs (Fig. 1; see also Table 4)

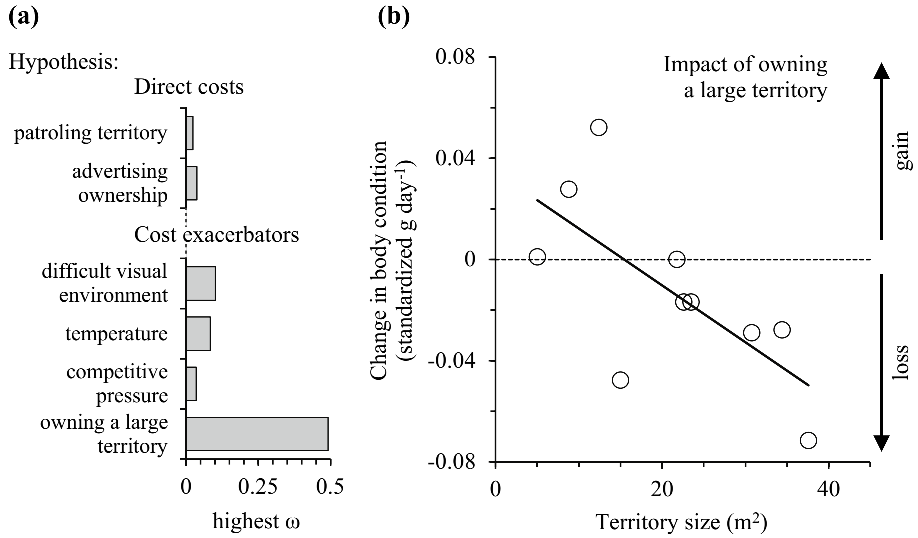

Fig. 3 A longitudinal empirical study of the cost of territoriality for ten male *A. gundlachi* lizards showing **a** the relative support for different hypotheses (see also Tables 1, 2) and **b** the association between changes in body condition of territory holders as a function of territory size

Table 4 Sequential exacerbators of the costs of territoriality as a second- or third-order function of the size of the territory occupied by male Puerto Rican lizard *Anolis gundlachi*

Paths to changes in body condition	ΔAIC_c	ω	$t_{\text{size of territory} \rightarrow x}$	$t_{x \rightarrow \text{body condition}}$
Size of territory → time on territory → body condition [*m*12]	4.0	0.11		
Size of territory → display perch use → body condition [*m*13]	0.0	0.81	−0.74	0.52
Size of territory → head-bob display rate → body condition [*m*14]	4.5	0.08		
Size of territory → number of male neighbours → time on territory → body condition [*m*15]	97.9	0.00		
Size of territory → distance to nearest neighbour → time on territory → body condition [*m*16]	99.5	0.00		
Size of territory → number of male neighbours → display perch use → body condition [*m*17]	90.5	0.00		
Size of territory → distance to nearest neighbour → display perch use → body condition [*m*18]	92.9	0.00		
Size of territory → number of male neighbours → head-bob display rate → body condition [*m*19]	97.0	0.00		
Size of territory → distance to nearest neighbour → head-bob display rate → body condition [*m*20]	98.2	0.00		

These path models were evaluated against each other using Shipley's AIC_c conversion of the C-statistic calculated for each model. Directed acyclic graphs (DAGs) are given in Fig. 4 (see also Fig. S4). The magnitude of putative casual links are presented as *t* values for the best-supported model

eightfold across the ten male lizards, and the lizard defending the largest territory experienced the greatest loss of condition (Fig. 3b). This effect of territory size on body condition was extremely large ($r = 0.69$, relative to a 'large effect' of 0.37).

Subsequent evaluation of feasible path models attempting to identify the manner in which territory size might impact body condition highlighted a single model ($\Delta\text{AIC}_c < 2.0$) centred on the putative mediating effect of perch use (or patrolling effort more generally; Table 4). However, the effect sizes of the underlying causal relationships in this model could not be statistically distinguished from zero (i.e., $t < 1.96$; Fig. 4).

Taken together, the size of a male's territory seems to exacerbate one or more costs yet to be measured in this system. The magnitude of the effect is consistent with those computed in the meta-analysis for patrolling effort, time away from other activities or advertising territory ownership (Fig. 2a), but all of these direct costs were largely considered in the models applied (Tables 3, 4). The effect size was also considerably higher than would be generally expected for an ectotherm (Fig. 2c), or for species that defend territories that monopolise various types of resources (Fig. 2d). The best territories for male lizards are likely to be those that overlap many females and offer refuges and sources of food. The abundance of all these recourses would presumably also increase with territory size. Yet, the magnitudes of the costs incurred by maintaining a large territory are more consistent with the defensive costs associated specifically with monopolising access to mates (Fig. 2d).

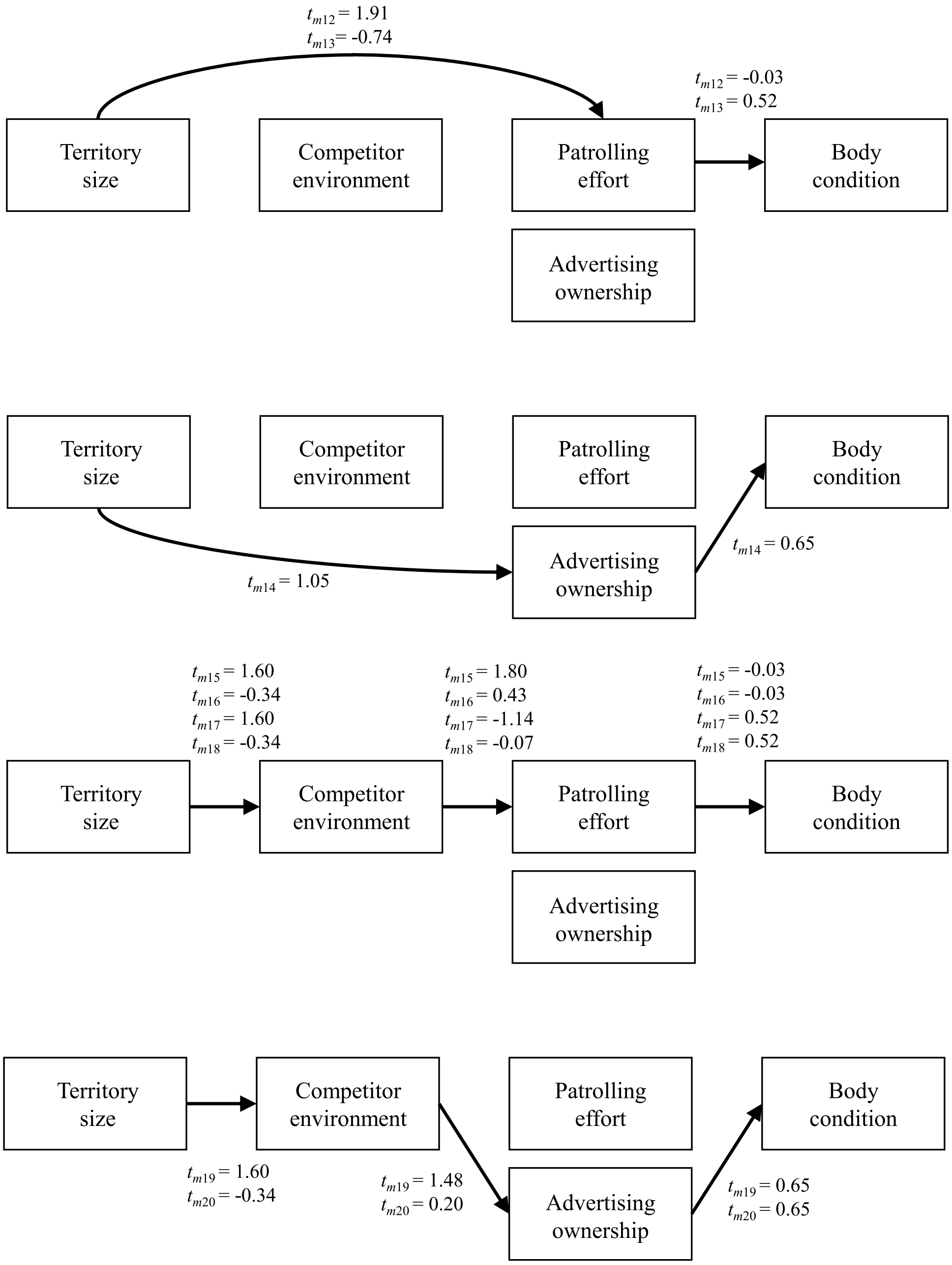

Fig. 4 Path models used to assess the impacts of territory size on the body condition of ten male *A. gundlachi* lizards through the mediating effects of competitive pressure, patrolling effort, and the frequency of territory advertisement display. Values associated with putative causal links are *t* values taken from associated path models (Table 4; see also Figure S4)

Discussion

If a single common cost can be identified from the review and meta-analysis, it would arguably be the amount of time that maintaining a territory diverts away from other activities (Fig. 2a). The time taken to maintain a territory can be expected to have various flow-on effects including reducing opportunities for feeding and other maintenance behaviours that affect growth and body condition in territory holders (Fig. 2b). Time also seems to be a factor in the context of how long a territory is maintained by its holder, in which all costs relating to territorial defence and maintenance might be expected to progressively accumulate over time (Fig. 2b) and again potentially affect a resident's overall growth and condition (Fig. 2c). The exception seems to be species that establish stable territories that allow the opportunity for territory holders to become familiar with their neighbours. Here, there would be an adaptive benefit for the evolution of cognitive mechanisms that allow territory holders to recognize individual neighbours that are less likely to intrude on territory boundaries, following an initial period of establishment. This "dear enemy" phenomenon (Table 2) should reduce the need for territory activity among familiar neighbours over time, with the adaptive benefit specifically conveyed through reduced territory costs as a function of the longevity and stability of territories.

Many species seem to have the capacity to track the identity of territory neighbours (Temeles 1994; Christensen and Radford 2018). The vast majority of empirical studies on this topic often open with the explicit statement that the phenomenon of dear enemy is expected to reduce the costs associated with territoriality. Out of the 60 studies on dear enemy initially uncovered as part of my review, only two met the criteria for inclusion in the meta-analysis (Fig. S1): Jaeger (1981) evaluated the number of injuries inflicted on familiar versus unfamiliar rivals in a salamander, while Siracusa et al. (2021) compared mortality rates of territory holders in squirrels surrounded by familiar versus unfamiliar territorial neighbours. In both cases, familiarity among individuals reduced the cost of territoriality (Fig. 2a; NB: the signs of effect sizes for these studies were reversed prior to aggregate estimates computed for Fig. 2b–d, such that the cost of defending a territory against unfamiliar rivals was benchmarked to situations where individuals were familiar with one another). Nevertheless, there is an obvious need for more study of the direct costs putatively minimised in species exhibiting behaviour consistent with dear enemy.

Other hypotheses such as advertising territory ownership, the physical defence of territories, and most notably competitive pressure—with the likely associated cost currencies of energetic expenditure and stress—were either modest in effect or negligible (i.e., 95% CIs overlap zero; Fig. 2a, b). The separate costs incurred from patrolling a territory and increased exposure to predation are less clear given these factors seem to have rarely been investigated (single studies in both instances). For example, the cost of patrolling was documented to have a very large effect on troops of chimpanzees (Fig. 2a, $r = 0.73$), because it reduced the time available for foraging and increased energetic expenditure through greater locomotion (Amsler 2010), but it was not influential in the empirical study of male *A. gundlachi* territorial lizards (Table 3; Fig. 3a).

Conversely, if a single gap in our current understanding can be identified, it would be the potential for predation while maintaining a territory, which was computed to have a modest effect ($r = 0.20$; Fig. 2a), but its generality was impossible to infer from a single study. Many behaviours associated with maintaining a territory are conspicuous—e.g., the production of advertisement signals—or might divert the attention of territorial holders from detecting potential predation threats—e.g., being distracted by monitoring territorial neighbours or challenging intruders. We know that conspicuous behaviour has the potential to expose animals to an increased likelihood of predation. For example, the elaborate morphologies of colour and ornamentation used to attract mates can inadvertently attract potential predators (Endler 1982; Martin and Lopez 2001; Rosenthal et al. 2001; Stuart-Fox et al. 2003). The production of loud calls for conspicuous sexual advertisement (Tuttle and Ryan 1981; Krams 2001), or possibly the elaborate movements used in territorial display (Steinberg et al. 2014), are also targets of predator eavesdropping to localise prey. In addition, other studies have shown attention devoted to social interactions which can detract from time spent in predator vigilance (Jakobsson et al. 1995; Cooper 1999; Diaz-Uriarte 1999). This suggests that any conspicuous behaviour or distraction associated with acquiring, maintaining, or defending a territory would increase the risk of predation and implies that predation should be a common cost of being territorial.

Yet, the empirical study of predation in the explicit context of territoriality (or even for aggressive behaviour more generally) was limited. Only one study reviewed (out of 42) examined predation. While my literature search was not intended to be exhaustive, it should be at least representative of the general research effort devoted to measuring different costs. Filling this gap in our understanding of the relationship between predation and territoriality will be challenging, because it likely reflects the difficulty in quantifying predation more generally. Of the studies mentioned in the previous paragraph, some are rare cases where predation could be documented in populations that were effectively closed and small (i.e., manageable in size) and could be compared to predator-free benchmarks (e.g., Endler 1982). Other studies have relied on acoustic playbacks of mating calls to predators in a captive setting (Tuttle and Ryan 1981) or attack rates on non-moving models of colorful prey deployed in a natural setting (Stuart-Fox et al. 2003). Translating some of these methods to the general context of measuring how territorial behaviour might increase the risk of predation would be difficult. Quantifying predator detection rates to playbacks of territorial vocalisations (sensu Krams 2001) or displays (Ord et al. 2021) is feasible, although likely limited in context. In the case of the single study included in the meta-analysis (Dias et al. 2010), the experimental design was creative and measured the likelihood of artificial bird nests being predated when placed inside the territories of male birds compared to areas outside of those territories. Given predation would appear to be a salient cost and one presumably shared across diverse taxa, more attempts in assessing its relationship with territoriality would be an obvious avenue for future research.

This would similarly be the case for studies attempting to document the consequences of familiarity among territory neighbours, where there is an explicit expectation that familiarity should translate directly into reduced costs, but has rarely been investigated (discussed above). The phenomenon of dear enemy has been predicted to be most likely in species that defend territories to monopolise access to mates, and least likely to occur in species defending access to food or other resources not directly linked to reproduction (Temeles 1994). This is based on the assumption that the greatest consequences for fitness are going to be those factors that directly impact mating opportunities. By extension, territories that monopolise access to mates will therefore be targets of considerable competition and cost. The premise of this prediction is at least consistent with the meta-analytic benchmarking reported in Fig. 2d, in which the greatest costs were experienced by species that use territories to ensure access to mates. In contrast, the magnitude of costs associated with territories defending food or refuges were small or statistically indistinguishable from zero. Any strategy that might reduce the costs associated with defending breeding territories would presumably be adaptive and these species would be the most obvious focal point for future research into neighbour recognition and its benefits for reducing the costs of territoriality.

However, the broader perspective obtained from my review of the literature and empirical study of Puerto Rican anole lizards is that cost is best considered as a compound variable. For example, time diverted from other activities in itself encompasses a range of potential factors (time away from foraging, mating, avoiding predators, etc.). The effect of territory size is another example, with the multitude of potential costs linked to space rather than time. The empirical study of territorial anole lizards tested four hypotheses typically examined by past studies, and the clearest outcome on male body condition was the combined costs that might be expected from owning a large territory (Fig. 3). Although this specific hypothesis received only marginal support in the meta-analysis (95% CIs just overlapped zero, based on two studies; Fig. 2a), it is consistent with the general idea that the cost of territoriality is best assessed as a broad, accumulative variable of (likely many) separate costs affecting various attributes (e.g., time budgets, growth, energy, stress, and mortality) over different time frames (immediate-to-long term).

Male anole lizards with larger territories are also likely to have access to a greater number of females. It is possible then that the dramatic reduction in body condition associated with owning a large territory in the empirical study might actually reflect the cost of reproduction specifically, rather than the defence of territory more generally. That is, males with large territories spent more time and energy courting and mating with many resident females, compared to males with small territories that can be expected to have overlapped fewer female home ranges. The analytical approach applied was explicit in comparing among models that considered both direct costs and factors that likely exacerbated those and other direct costs (through an unquantified 'variable $X_{1\text{-}i}$'; Fig. 1). A subsequent path analysis considered the potential impact territory size might have on competitive pressure, patrolling effort, and the need for frequent energetically costly territorial display, but failed to identify any compelling effects. This suggests that territory size had influenced the body condition of territory holders through other unmeasured factors, which might include costs associated with reproduction. This model selection approach provided a powerful means of not only evaluating alternative hypotheses concurrently, but the identification of cost(s) not explicitly measured in the field. Follow-up study can now focus on determining what those specific costs associated with owning a large territory might be in this species.

The negative effect of owning a large territory aligns with classical assumptions of how territoriality impacts condition (e.g., Clutton-Brock and Albon 1979) and counters many recent food supplement experiments reporting a positive association between condition and territory size (see introduction). It is important to note, however, that while male lizards with the largest territories declined most in condition, these males were generally in better condition at the start of the study (i.e., there was a positive relationship between male starting condition and territory size; $r = 0.48$, see Fig. S3) and were therefore in a superior position at the outset to handle the increased costs associated with maintaining a large territory. The evaluation of costs is therefore contingent on comparing against the right benchmark.

In addition, the currency of cost measured—the *y* variable examined in statistical analyses—will affect which hypothesized costs can be appropriately tested. The relevance of measuring the "right" currency for a given hypothesis of cost is exemplified in the descriptions of each hypothesis in Tables 1 and 2. Different hypotheses are likely associated with different currency outcomes and selecting a range of currency measures would presumably provide better resolution of what those costs—and their magnitude—might be for territorial animals. For example, the cost of patrolling by male *A. gundlachi* might have been measured through its direct effect on feeding rates or coupling frequency with females. Nevertheless, body condition is expected to reflect various hypothesized costs (e.g., Fig. 3a) and was the most common currency evaluated by many other studies as well (Fig. 2b), allowing comparative benchmarking to other territorial species. However, it would have not been particularly useful for evaluating predation risk.

Both the meta-analysis and empirical study showed low-to-no effect of changes in competitive pressure on territory holders. The two new hypotheses partly inspired by the natural history of *A. gundlachi* used in the empirical study similarly received little support (Table 3), despite both the signal environment and temperature being important influences on the territorial activity of these lizards (Ord et al. 2016; Ord and Stamps 2017). In the case of temperature, the result was broadly consistent with the lack of difference in the magnitude of costs experienced by ectotherm and endotherm species in the meta-analysis (Fig. 2c). This implies that temperature-dependent metabolic processes, which affect energy expenditure and activity, do not have tangible outcomes on being territorial. This is in turn consistent with the observation of territoriality in diverse species, from some of the smallest invertebrates (e.g., *Drosophila*: White and Rundle 2015) to the largest mammals (e.g., lions; Packer et al. 2005).

The cost of territoriality is best accounted for empirically and theoretically as the collective outcome of various adverse effects and events, especially those incurred because of the amount of time required to maintain a territory (Fig. 2a), but also the consequences of a territory's gross size (Fig. 3). Change in body condition was the most common currency measured by studies, but as a general measure, it captured largely modest effects compared to changes in time budgets, feeding rates, or growth rate. Energy expenditure and physiological stress were also common currencies measured by studies but generally reported low effects, which contradicts the common perception that energy and stress are dominant costs incurred from territorial behaviour. More generally, I illustrate an analytical approach that can assess the level of evidence for various hypotheses in a single unified framework and using observational data obtained from free-ranging animals. By providing a means to evaluate multiple hypotheses concurrently, this framework would be especially useful for identifying the most plausible hypothesis to then focus more detailed investigation or subsequent experimental work hoping to establish causality.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-021-05068-6.

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Author contribution statement TJO conceived, designed, and executed the study and wrote the manuscript. No other person is entitled to authorship.

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Availability of data and materials All data associated with this study is publicly available through the Dryad digital data repository (https://doi.org/10.5061/dryad.r7sqv9sd1).

Code availability All code associated with this study is available from the author (t.ord@unsw.edu.au).

Declarations

Conflict of interest There are no conflicts or competing interests associated with this work.

Ethics approval The empirical work outlined in this paper was covered under Animal Use and Care Protocols 05-11652/15243 from the Institutional Animal Care and Use Committee of the University of California at Davis.

Consent to participate Not applicable.

Consent for publication Not applicable.

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