

ANIMAL TERRITORIALITY, PROPERTY, AND ACCESS:

A COLLABORATIVE EXCHANGE BETWEEN ANIMAL BEHAVIOUR AND THE SOCIAL SCIENCES

Ambika Kamath^{1,2,3} and Ashton Wesner^{2,4}

1. Miller Institute for Basic Research in Science, University of California Berkeley.
2. Department of Environmental Science, Policy, and Management, University of California Berkeley.
3. Author for correspondence: ambikamath@gmail.com.
4. Department of History, University of California Berkeley.

1 Abstract

2 Territoriality is central to animal behaviourists' understanding of many facets of animal
3 behaviour, including resource acquisition, space use behaviour, communication, and mating systems.
4 However, the term itself—how it is conceptualized and defined—has long been nebulous and
5 contentious. Here, we ask if juxtaposing debates about territoriality from animal behaviour with
6 parallel discussions of territoriality from the social sciences can offer a historically- and
7 sociologically-informed path out of the conceptual gridlock in which animal territoriality has been
8 located for decades. We delineate two key problems with territoriality identified in the animal
9 behaviour literature: First, that it focuses on how animals are expected to behave rather than how
10 they actually behave and second, that it assumes rather than demonstrates the function of, and
11 specific relationships among, individuals. We then link these problems to social scientists'
12 theorizations of the difference between property and access—whereas property is focused on how

13 people are expected to behave under juridical-legal rules governing resource use, access focuses on a
14 wide array of means by which people actually access resources. We thus argue that longstanding
15 problems with animal territoriality have arisen due to implicitly embedded notions of property and
16 ownership. Our juxtaposition raises two further problems with territoriality—first, that territoriality
17 unwarrantedly serves to naturalize the authority of some individuals as territory “owners” and casts
18 others (“intruders”, “sneakers”) as transgressors, and second, that conceiving of ownership is
19 unfeasible in animal societies lacking the particular juridical-legal institutions that establish and
20 enforce property rights. Instead, we advocate for an access-based approach that will obviate these
21 problems. Ultimately, we argue that the theory of access—as developed in social science literatures
22 on spatial and relational resource use—will allow for a fuller and more nuanced understanding of
23 variation in animal behaviour than that afforded by current dominant notions of territoriality.

24

25 **Introduction**

26 Territoriality is a powerful framework in animal behaviour, motivating and lending context
27 to research on myriad aspects of animals’ biology, including resource acquisition, space use
28 behaviour, communication, and mating systems (Noble 1939, Carpenter 1958, Orians 1969, Emlen
29 and Oring 1977, Maher and Lott 1995, 2000). In spite of, or perhaps because of, this widespread
30 utility, territoriality is challenging to define. In fact, from a historical perspective, the concept of
31 territoriality has been problematic in part because animal behaviourists have disagreed about
32 territoriality for decades—for example, Emlen (1958), Waser and Wiley (1979), Kaufmann (1983),
33 Maher and Lott (1995), Stamps (1994), Bush and Simberloff (2018), and Kamath and Losos (2017,
34 2018a) have all grappled with similar questions of how to conceive of, define, and demonstrate
35 territoriality in animals even as empirical research based on territoriality has continued unabated. In

36 this paper, we present a historically- and sociologically-informed path out of the conceptual gridlock
37 underlying research on animal territoriality. Specifically, in addressing some of the history of debates
38 on territoriality, we:

39 (1) Discuss past definitions of territoriality (Kaufmann 1983, Maher and Lott 1995) to
40 illustrate that animal territoriality has long been both nebulous and contentious.

41 (2) Delineate two central problems with territoriality: First, it focuses on how animals
42 are expected to behave rather than how they actually behave, and second, it assumes rather
43 than demonstrates the function of, and specific relationships among, individuals (Emlen
44 1958, Kaufmann 1983, Stamps 1994). We describe how these problems with territoriality
45 manifest in studying mating systems, an example we return to throughout the paper.

46 (3) Present potential reasons for, and solutions to, the problems of territoriality by
47 juxtaposing literature on animal territoriality with literature on the concepts of property and
48 access from the fields of critical social theory, political theory, and geography (Sack 1983,
49 Rose 1985, Ribot and Peluso 2003, Blomley 2016). Specifically, we argue that animal
50 behaviourists have implicitly and explicitly incorporated aspects of property and ownership
51 from human societies into animal territory, a conflation that is unwarranted and problematic.
52 We examine how social scientists have grappled with similar problems of conflating property
53 and resource use, and draw from their theorizations to suggest that instead of enrolling a
54 theory of property to better define animal territoriality (Strassmann and Queller 2014),
55 animal behaviourists might clarify and strengthen studies of animal territoriality by moving
56 toward a theory of access (Ribot and Peluso 2003).

57 Our overarching motivation in writing this paper is to recognize that, notwithstanding
58 scientists' aspirations towards objectivity, scientific practices are embedded within a cultural and

59 social milieu (Haraway 1989). Research in animal behaviour is especially ripe for sociocultural
60 analysis because of the similarities between the concepts being studied and the lives of the people
61 studying them (Zuk 1993, Fausto-Sterling 1997, Lawton et al. 1997, Tang-Martinez 1997). In
62 particular, research on animal territoriality is influenced by not only “the sort of resources that are
63 limiting...and the animal’s behaviour” but also by “tradition [and] opinion” (Maher and Lott 1995,
64 p. 1582), encouraging us to turn to the social sciences to better understand how sociocultural
65 traditions and opinions may have shaped scientific studies of animal territoriality.

66 **Methodology**

67 In this study, we draw connections between debates in animal behaviour and in the social
68 sciences surrounding the definitions and theorizations of territory, to tackle the conceptual gridlock
69 surrounding animal territoriality in a historically- and sociologically-informed way. This paper is the
70 outcome of a collaboration between a behavioural ecologist (AK) and an interdisciplinary social
71 scientist (ABW), wherein we initially exchanged and discussed readings from each of our areas of
72 scholarship to find shared language and ideas on the concepts of territoriality (animal behaviour:
73 Kaufmann 1983, Strassman and Queller 2014; sociology: Ribot and Peluso 2003). In response to
74 questions arising during our initial conversation, we included further literature from the social
75 sciences (critical social theory, political theory, and geography; Sack 1983, Rose 1985, Blomley 2016)
76 into our discussion. We also broadened our discussion of animal territoriality to include Emlen
77 (1958), Emlen and Oring (1977), Waser and Wiley (1979), Kaufmann (1983), Stamps (1994), and
78 Maher and Lott (1995), six touchstone papers that review and theorize about how animal
79 behaviourists use the term “territoriality.” These discussions formed the basis for writing this text.
80 Our approach was a less-formal version of a methodology for interdisciplinary research between

81 biologists and social scientists, detailed in Wesner (2019), that hinges on mutual engagement (Willey
82 2016) via exchanged readings followed by focus-group discussions.

83 Our primary focus in this text is not the behaviour of animals but the ideas and practices of
84 scientists studying animal behaviour. We therefore include quotations from the literature more
85 frequently than a typical scientific paper, because these quotes constitute the basis on which we
86 discuss how scientists have conceived of territory. Further, for clarity and convenience, we use the
87 word “animals” to refer to non-human animals only.

88 **Some definitions of territory in animals and humans**

89 Both animal behaviourists and social scientists have long considered how to define territory
90 and territoriality. In both areas of scholarship, the mainstream view characterizes territory as a
91 “defended area,” and territoriality as the “defence of area” (Sack 1983, Kaufmann 1983, Maher and
92 Lott 1995). These definitions appear straightforward, but territoriality is, in fact, far from simple.

93 In a review of how territory is defined in vertebrates, Maher and Lott (1995) found 48
94 different definitions of the term, most of these implicit—only 12% of papers in their sample
95 included an explicit definition. The three most common conceptual definitions were “(1) defended
96 area, (2) exclusive area and (3) site-specific dominance” (Maher and Lott 1995, p. 1583). The authors
97 note that whether or not a species could be classified as territorial depended on the conceptual
98 definition employed; for instance, in a low-density population, individuals in a species may
99 effectively occupy exclusive areas without defending them and would thus be territorial under the
100 second, but not the first, definition.

101 Moreover, “territoriality is a hypothetical construct, and its only reality lies in the operational
102 definition” (Maher and Lott 1995, p. 1588). The operationalization of these conceptual definitions

103 can reveal further nuances and complexities. For example, attempting to quantify territory using the
104 conceptual definition of “defended area” raises the following questions: For how long does a
105 particular area need to be defended in order to count as a territory? How much of an individual’s
106 time must be spent defending this area, or what proportion of its home range must the area
107 comprise? What behaviours actually constitute defence—is it behaviour at the boundaries of the
108 territory and if so, how are those boundaries determined? Is any aggressive or display behaviour
109 indicative of territoriality? Must the defence of a territory be effective i.e., how successful must an
110 individual be at excluding others from an area? How animal behaviourists choose to answer these
111 questions, and thereby construct an operational definition of territory in the context of a particular
112 study, depends upon the taxon and research question being addressed, as well as logistical
113 considerations. This leads to a wide variety of phenomena falling under the umbrella of territoriality,
114 making comparisons across studies, taxa, and contexts challenging (Linklater 2000). Maher and Lott
115 (1995, p. 1589) thus exhort animal behaviourists to be “consistent, or at least explicit, in their
116 terminology.”

117 In response to these definitions focused on an area as the object of defence and exclusion,
118 both natural and social scientists have advocated for more nuanced definitions that instead focus on
119 how territory is socially constructed through interactions among individuals (e.g. “site-specific
120 dominance,” the third most common conceptual definition in Maher and Lott [1995]). Sack (1983,
121 p. 55) defined human territoriality as “the attempt to affect, influence, or control actions and
122 interactions (of people, things, and relationships) by asserting and attempting to enforce control
123 over a geographic area,” or more simply as a “strategy for establishing differential access to things
124 and people.” Sack’s (1983) characterization resonates with definitions of animal territory that
125 similarly focus on the relationships among individuals from which space-use or resource-use
126 patterns emerge. Kaufmann (1983, p. 2), for instance, describes territoriality as “one form of social

127 dominance,” and defines a territory as “a fixed portion of an individual’s or group’s range in which it
128 has priority of access to one or more critical resources over others which have priority elsewhere or
129 at another time” and adds, “this priority of access must be achieved through social interaction”
130 (Kaufmann 1983, p. 9). This distinction—between defence or exclusion versus social interactions as
131 a basis for conceptualizing territory—provides a route into understanding two problems central to
132 animal territoriality.

133 **Some problems with territoriality revealed by conceptual examination**

134 A powerful critique of animal (specifically bird) territoriality was developed by Emlen (1958).
135 He made the case that the definition of a territory as a “defended area” constrained research on bird
136 behaviour, because it was a misleading assumption to describe birds as defending areas *per se*. Rather,
137 his observations suggested that while some individual birds were aggressive towards and perhaps
138 dominant over other individuals in some areas (consistent with Kaufman’s [1983] definition of
139 territory described above), there was little “justification for including a purely speculative assumption
140 that the area carries special significance to the bird as an object to be defended” (Emlen 1958, p.
141 352). In other words, Emlen (1958) argued against automatically inferring the defence of an area (or
142 other resources) from aggressive behaviour, as many studies of territoriality do.

143 Moreover, Emlen (1958) suggested that most ornithologists’ conception of territory conflate
144 definition with hypothesis. It is possible to *hypothesize*, and then test the hypothesis, that an animal
145 defends an area and is thus territorial. However, when defined as “the defence of an area,” the
146 concept of territoriality is constructed such that *applying* the concept to a particular taxon depends
147 upon *assuming* that the hypothesis of defence is true. As Emlen (1958, p. 352) put it, “assumptions
148 are natural features of hypotheses proposed for experimental testing, but have no place as integral
149 parts of a functioning concept.” In his view, a useful concept of territory would focus on “doings

150 and happenings rather than objects and entities.” Thus, the first problem with common scientific
151 usage of territoriality is that it perpetuates a disconnect between what *is* versus what *should be*. Rather
152 than focusing attention on how social interactions actually unfold in spatial ways (what *is*),
153 territoriality is often operationalized in prescriptive ways (what *should be*) that rely on assumptions of
154 how animals relate to and occupy a predetermined type of space.

155 Emlen’s (1958) critique resonates deeply with an observation made by Sack (1983) in his
156 foundational characterization of human territoriality. Sack (1983, p. 59) stated that the notion of
157 territory shifts attention away “from the relationship between controller and controlled” and
158 towards the space itself, “as when we say “it is the law of the *land*” or “you may not do this *here*”
159 [emphasis in original].” This shift is precisely what Emlen (1958) cautions against.

160 This difference between what *is* and what *should be* is especially salient in considering
161 territoriality in relation to mating systems. In the classic paper linking territory to polygyny, Emlen
162 and Oring (1977) state that whether a species *can be* polygamous depends on whether multiple mates
163 are economically monopolizable; whether the species *is in fact* polygamous depends on its ability to
164 capitalize on this potential for mate monopolizability. They link this potential for, and realization of,
165 polygamy to various ecological, social, and physiological factors. In so doing, they build a unified
166 theory of animal mating systems based on a territorial notion of monopolization by defence—not
167 necessarily of a delimited area, but of mates themselves. Thus, even though most animals are not
168 classified as territorial, territoriality is deeply embedded in our understanding of animal mating
169 systems writ large. Within this framework, behavioural descriptions of mating systems are essentially
170 predictions of what mating patterns *should be* if animals adhere to rules of defence for the purpose of
171 mate monopolization. However, the advent of genetic tools to determine paternity revealed that
172 actual patterns of animal mating (what *is*) were starkly inconsistent with expected mating patterns

173 derived from behavioural observations under a territorial framework (Avisé et al. 2002, Griffith et al.
174 2002, Uller and Olsson 2008, Boomsma et al. 2009). Thus, inferring mating patterns through a
175 territorially-derived lens frequently fails to predict or explain animals' actual mating behaviour;
176 subsequent attempts to explain these departures from expected behaviours are posed as exceptions
177 to the territorially-derived norm (e.g. Cockburn et al. 2013).

178 The second problem with territoriality is that it leads animal behaviourists to assume rather
179 than demonstrate the reasons for particular behaviours, constricting these reasons to a small subset
180 of all possibilities (Stamps 1994, Tang-Martinez 2014). Consider, for example, Maher and Lott's
181 (1995, p. 1587) description of the function of communication in relation to territoriality in birds:
182 "Territory in birds was most commonly defined as defended area...Most bird studies involved
183 passerines that advertise their territories by singing. Singing provides a relatively easy way to quantify
184 and identify territoriality; in low visibility habitats, measuring [the] amount of singing is easier than
185 counting numbers of intruders moving through vegetation." This example shows that alternative
186 explanations for what information individuals might communicate when singing (e.g. simply
187 communicating identity), or why they might behave aggressively (e.g. to establish rank in a
188 dominance hierarchy), are rarely considered once a species is believed to be territorial (Emlen 1958,
189 Linklater 2011). This means that, under the paradigm of territoriality, communication is assumed to
190 have specific territorial function, be it advertising territory ownership (Rose 1985) or communicating
191 imminent aggression towards would-be intruders; similarly, aggression is assumed to serve the
192 function of defence.

193 A particularly salient way in which territoriality prompts animal behaviourists to integrate
194 assumptions into the conceptual foundations of their work while also restricting possible
195 interpretations of animals' behaviours is in the classification of individuals into particular roles

196 within a territorial framework (Stamps 1994). Consider, for example, the ubiquitous use of the term
197 “intruder” to describe an individual who moves into an area that has been assigned as the territory
198 of another (Kaufman, 1983; Maher and Lott, 1995). Describing that individual *as an intruder* (as
199 opposed to, say, *a visitor*) leads us to expect an antagonistic interaction between the two individuals.
200 The two individuals’ relationship to one another and to the space they occupy are attributed to the
201 centrality of a possessive figure (the “territory owner”) rather than necessarily derived from actually
202 observed behaviours.

203 To illustrate how territoriality assumes relationships between individuals in the context of
204 mating systems, consider another term, “sneaker.” Sneakers are males that enter dominant males’
205 territories to covertly attempt to mate with females within the territory (or otherwise seek to covertly
206 mate with females thought to be in the “possession” of a dominant male; Taborsky 1994). An
207 animal behaviourist mapping the territories of individual males is especially likely to assign the label
208 of “sneaker” to a comparatively smaller male who enters an area assigned as the territory of another
209 (usually larger) male, even if the two males do not interact with one another. Indeed, the term
210 “sneaker” suggests that the first male will behave surreptitiously to avoid interacting with the second
211 male. A “sneaker” thus can be seen as not only a transgressor of territorial boundaries but also a
212 perpetrator of infidelity (e.g. Jones et al. 2001), reinforcing an underlying assumption that only the
213 dominant, territorial figure has legitimate claim to a space or the contents of that space.

214 When non-territorial or non-dominant individuals are defined primarily in terms of their
215 purported transgressions against dominant, territorial males, it can become difficult to interpret their
216 behaviour in any other light (Ah-King 2007). In the Coho salmon, where males belong to either the
217 “jack” or “hooknose” morphs, the mating strategy of the smaller jack males has traditionally been
218 described as “sneaking” or “parasitic” and their continued existence described as “problematical”

219 (Gross 1985, p. 47). As is common in species with comparable male phenotypic variation, animal
220 behaviourists had assumed that dominant hooknose males were females' preferred mates. However,
221 in a radical reframing of Coho salmon mating strategies, Watters (2005) hypothesized that females in
222 fact prefer jack males and cooperate in mating with them, whereas less-preferred hooknose males
223 coerce females into mating. In this case, Watters (2005) opted not to delimit female individuals as
224 objects of defensive territoriality, nor assume the centrality of a dominant "territorial" male
225 individual. Rather, he tested a hypothesis that opened a broader range of possibilities for how social
226 relations between individuals are spatialized, thus contributing novel findings to the study of his
227 system. Watters' (2005) observations of Coho salmon behaviours are consistent with his
228 hypothesis—females spent more time preparing their nests and spawned for longer in the presence
229 of jacks, and in situations where a jack was chased away from a nest by a hooknose, the female
230 spawned soon after the jack's return.

231 **Property and access in human and animal contexts.**

232 *Animal territory as property?*

233 Just as animal behaviourists have contended with a disconnect between assumptions about
234 animal behaviour borne of socioculturally imbued concepts (what *should be*) and animal behaviours
235 actually observed (what *is*), so, too, have social scientists grappled with the distinction between the
236 concepts of *property* (what *should be*) and *access* (what *is*). This theoretical conversation among social
237 scientists can illuminate—even in the study of animals—the limitations of conceiving territory as a
238 fixed area that is defended by individual(s) and bounded by rights or rightful relations (property).
239 New analytical possibilities emerge when animal behaviours are instead conceived of through a
240 rubric of access to other individuals, spaces, and resources.

241 Ribot and Peluso (2003, p. 153) first defined access “as the ability to benefit from things—
242 including material objects, persons, institutions, and symbols. By focusing on *ability* rather than *rights*
243 as in property theory, this formulation brings attention to a wider range of social relationships that
244 can constrain or enable people to benefit from resources without focusing on property relations
245 alone...The concept of access...aims to facilitate grounded analyses of who actually benefits from
246 things and through what processes they are able to do so [emphasis in original].” Thus, the
247 theoretical framework of access insists that a researcher investigate processes, relationships, and
248 behaviours that determine how resources are used. The call for social scientists to focus on how
249 people interact to benefit from resources is very similar to calls by Emlen (1958) and Kaufmann
250 (1983), described above, to focus on “doings and happenings” rather than “objects and entities” in
251 the study of animal behaviour.

252 Social science scholars have turned to the theory of access in response to the limitations of
253 property frameworks for really understanding how people benefit from, or are excluded from,
254 material and social resources. Property, they have demonstrated, maintains a focus on the objects or
255 spaces that are owned, and specifically, on the formal rules surrounding who is and is not allowed to
256 use the owned entities. These rules are expressed in language on property through notions of the
257 owners’ *rights*. Consider, as an illustration, Blomley’s (2016, p. 594) description of land as property in
258 human society: “the rights of the owner (to use, occupy, alienate, and so on) apply uniformly across
259 and exclusively within this space. It is also presumed that these rights attach to an individual owner
260 who therefore is assumed to command all the resources within this designated space. The owner is
261 also assumed to have the right to govern the access of others...to this space, allowing conditional
262 access or denying it entirely.” Yet social scientists have long documented that juridical-legal rights, or
263 even informal social agreements, do not in fact determine how humans benefit from objects,
264 resources, spaces, or relationships. A property framework, for example, does not best enable social

265 scientists to understand how communities collectively manage commons (Ostrom 1990), prioritize
266 cultural norms of resource sharing over state-sanctioned legal titles (Walker and Peters 2010), or
267 whether the named property-holder on a land title is actually the same person farming the material
268 plot (Peters 2010). Theories of access, on the other hand, enable researchers to turn to the informal
269 agreements, the grounded-practices, and the actual use or occupation of different spaces to
270 understand how, when, and where different individuals benefit from resources across time and
271 space.

272 We suggest that these parallel arguments in the natural and social sciences—about what
273 *should be* and what *is*, and the undue focus on possessive functions and interactions in both animal
274 territory and human property—are more than just similar. Rather, we contend that notions of animal
275 territoriality have incorporated aspects of classically defined property (see Blomley 2013 for more
276 capacious cultural engagements with the idea of “property”), and that these incorporations
277 contribute to the problems with territoriality described above. We show that by paying close
278 attention to social scientists’ differentiation of property and access, animal behaviourists will be
279 better able to disambiguate and resolve the most challenging confusions of territoriality.

280 Burt (1943), a key early paper on territoriality that has been cited over 2500 times and
281 represents a foundational paper in the study of animal territoriality, overtly conflates animal territory
282 and human property. The paper opens with the following conceptual assertion about territoriality
283 (Burt 1943, p. 346):

284 “The behavioristic trait manifested by a display of property ownership—a defense of
285 certain positions or things—reaches its highest development in the human species. Man
286 considers it his inherent right to own property either as an individual or as a member of
287 society or both. Further, he is ever ready to protect that property against aggressors, even

288 to the extent at times of sacrificing his own life if necessary. That this behavioristic pattern
289 is not peculiar to man, but is a fundamental characteristic of animals in general, has been
290 shown for diverse animal groups.”

291 Two subsequent papers—Stamps (1994) and Strassman and Queller (2014)—continued to
292 centre notions of property and ownership in discussions of territoriality, and thereby highlight the
293 problems of animal territoriality that we describe above. In a tour-de-force critique of the many
294 untested assumptions of animal territoriality, Stamps (1994, p. 176) described the “economic
295 approach to the problem of territory function,” which focuses on costs and benefits of territory
296 defence and thus readily lends itself to a framework of ownership. She suggested that this economic
297 approach allowed for generalized discussions of territoriality across many different taxa but also that
298 it “led to a reduction in the number and type of environmental and social factors thought to affect
299 the benefits or costs of territorial behavior.” In particular, “the ascendancy of the economic
300 approach...affected assumptions about the effects of conspecifics on one another” (Stamps 1994, p.
301 178). Earlier animal behaviourists “were willing to entertain the possibility that conspecifics might
302 have a positive as well as a negative effect on one another in territorial species.” These positive
303 effects could include the formation of social groups that aid in collective defence, synchronized
304 reproduction, and the attraction of mates. But “with the advent of the economic approach, the
305 emphasis shifted to the competitive effects of conspecifics on one another. Neighbours, floaters,
306 intruders etc., all entered the equation in the same place, as factors contributing to the cost of
307 territorial defense.” Stamps (1994) seems to imply, but does not state outright, that territoriality’s
308 problem of assuming and constricting function and interactions arises *because of* its incorporation of
309 economic notions of costs and benefits. While a straightforward focus on costs and benefits does
310 not necessarily preclude consideration of positive interactions, Stamps’ (1994) critique resonates with
311 an ownership-based understanding of social interactions that prompts disproportionate attention to

312 antagonistic interactions motivated by, and costs incurred due to, the maintenance or transgression
313 of possession.

314 The lens of property, along with that of privatization, has been applied explicitly to animal
315 territories by Strassman and Queller (2014, p. 306), who suggest that territory “is perhaps the best-
316 recognized form of privatization” in animals, and “can be defined as property in the form of an area
317 that an organism controls, uses, and defends.” Such an explication is consistent with Emlen and
318 Oring’s (1977) sense of territory as a means for monopolization. By making these linkages between
319 the concepts of animal territory and human property explicit, and by considering this connection
320 obvious even as they acknowledge its limits, Strassman and Queller (2014) demonstrate both the
321 prevalence of and the problems with property-based notions of animal territoriality.

322 In particular, their discussion of mating systems clearly demonstrates how territory shifts the
323 discourse surrounding animal behaviour towards what *should be* and away from what *is*. As Strassman
324 and Queller (2014, p. 306) put it, when describing how territorial male birds’ behaviour is inferred to
325 serve the purpose of “privatizing” reproductive access to females, “such privatization is *imperfect*, as
326 shown for example, by the often high frequencies of young in the nests that are not the progeny of
327 the attending male...a large part of the challenge for territorial males is that they are attempting to
328 privatize a living conspecific that may have conflicting interests [emphasis added].” In this context,
329 territoriality has served to naturalize and reinforce the notion that individuals take possession of
330 other individuals (and specifically, that males take possession of females). Moreover, the discrepancy
331 between expected and observed mating patterns is seen by Strassman and Queller (2014) as animals
332 executing territoriality *imperfectly*, and not as a shortcoming of territoriality itself as a means of
333 understanding animal behaviour. In other words, attention remains focused on what animals are
334 expected to be doing under the rules of territory and how they are or are not conforming to these

335 expectations, at the cost of developing novel non-territorial frameworks to understand how animals
336 actually behave (e.g. Kokko and Mappes 2013, Kamath and Losos 2018b). Exactly as Emlen (1958)
337 warned, territoriality leads “the study of natural phenomena [to be] subordinated to the study of
338 intellectual creations.”

339 *Problems revealed by the parallels between animal territory and human property*

340 Pondering the parallels between animal territory and classic notions of property in humans
341 reveals two other potential problems that may have contributed to the challenge of conceptualizing,
342 defining, and effectively using territoriality in the study of animals. We pose these problems here as
343 starting points from which animal behaviourists could embark on further critical inquiry, asking
344 whether and how these problems have influenced the ways animal behaviourists construct research
345 questions and interpret data on animals’ space use, movement behaviour, communication, resource
346 acquisition, social interactions, survival, and reproduction.

347 First, notions of property embedded within the concept of animal territoriality serve to
348 naturalize both authority and discipline. In other words, rather than authority and discipline being
349 recognized as power-laden social relationships emerging from human societies, they are envisioned
350 as innate qualities of animal behaviour emerging directly from “nature’s order” (Haraway 1991).
351 Think again of “intruders”—it seems clear that when we think of “intruders” as crossing the
352 boundaries of another animal’s territory, then we may, however unintentionally, conceive of the
353 intruder as transgressing the *rights of a property owner*. The term “intruder” evokes the idea of trespass,
354 or the “act of unlawful entry upon land in another’s possession,” an act that, in many current
355 conceptions of property law “is actionable even though no actual damage is done: the mere act of
356 boundary transgression is sufficient” (Blomley 2016, p. 597). In this way, the intruder’s actions take
357 on a sense of being “unlawful,” in opposition to the actions of a territory-holder that are configured

358 as the “norm.” Similarly, “sneaker” males are conceived of as subverting the rules surrounding more
359 dominant males’ naturalized possession of females. As we saw above in the example of Coho
360 salmon, framings of animal behaviour that focus on possessive male-female interactions potentially
361 led to animal behaviourists ignoring, for decades, the possibility that females actually might benefit
362 more from mating with the subversive “sneaker” male than with dominant males whose actions are
363 considered the norm (Watters 2005). Such framings project onto animals the notion of an
364 individual’s *inherent right* to exclude another from a particular space or particular interactions—the
365 sociocultural valuation of private property is naturalized. A conception of territoriality that implicitly
366 incorporates notions of property can lead animal behaviourists to interpret animal behaviours as
367 obviously indicative of ownership, without necessarily considering alternative interpretations and
368 frameworks that do not hinge on ownership.

369 The non-neutral subversive and transgressive connotations of terms such as “intruder” or
370 “sneaker” are rarely explicit and likely not intended, but they are nonetheless consequential. As
371 Gowaty (1982) illustrates through her analysis of the term “rape” in sociobiology, using words that
372 have emotional resonance in human discourse as technical terms in research on animals comes with
373 multiple downsides, including imprecision, the introduction of bias, and unwarranted sensationalism
374 (see also Haraway 1989, Mesnick 1997, Lawton et al. 1997, Tang-Martinez 1997, and Elgar et al.
375 2013 for discussions of the consequences of anthropomorphic terminology in animal behaviour).

376 A second important problem with incorporating notions of property into animal territory is
377 that the existence of property, which is often conceptualized as a “bundle of rights” (Maine 1917),
378 depends upon the existence of historically specific juridical-legal institutions that enshrine rights and
379 impose sanctions when rights are transgressed (Rose 1994, Blomley 2016). Yet when studying the
380 spatial elements of animal behaviour and communication, scientists do not purport to identify or

381 examine animals' formal institutions, mechanisms of government, or legal enforcements and
382 protections of rights. Strassman and Queller (2014, p. 308) acknowledge that “nonhumans do not
383 generally have the higher-level institutions and each individual must therefore rely on itself or its kin
384 group.” However, they maintain that property rights in animals exist nonetheless, suggesting that
385 “although only humans have higher-level social institutions that protect property, other organisms
386 may sometimes have evolved recognition of ownership and hesitation to challenge it.” Strassman
387 and Queller (2014, p. 307) propose that “physical force, or the threat of it, is perhaps the primary
388 method of privatization,” and therefore of property maintenance in animals. This reveals the
389 problems with embedded notions of property in territory—while the threat of force could be a
390 (potentially costly) strategy for maintaining *access* to resources (Ribot and Peluso, 2003), on its own it
391 is insufficient for establishing, enshrining, and enforcing *rights*. The example cited by Strassman and
392 Queller (2014) to illustrate putative ownership is that territory “owners” fight more readily than
393 “intruders.” But such behaviour is explicable without invoking ownership, simply by considering
394 access. For example, an individual that is familiar with an area may benefit more from remaining in it
395 than would an unfamiliar individual, and thus may be more inclined to fight for access to its
396 resources. The theory of access (Ribot and Peluso 2003) offers animal behaviourists a way forward
397 for understanding animal behaviour that is not constrained by notions of property.

398 **A mode of animal behaviour analysis informed by theory of access**

399 According to the theory of access (Ribot and Peluso 2003), different individuals and groups
400 are understood to benefit from access to resources in different ways for different reasons; property
401 ownership is conceived of as one of many avenues or strategies for accessing resources, as opposed
402 to being the fundamental determinant. Thus, when viewed through an access-based lens, animal
403 behaviours are no longer coupled *a priori* with legal or moral connotations. For example, animals

404 need no longer be categorized as territory “owners,” which are implicitly ascribed property rights, or
405 as “intruders” or “sneakers” that transgress those rights. The notion of rights would only be
406 pertinent in those species that are demonstrated to have juridical-legal institutions capable of
407 enforcing rights—access *allows for* but does not *demand* ownership or rights-based exclusion. Thus,
408 the lens of access immediately addresses the two problems of territoriality that this paper has
409 illuminated through the juxtaposition of the natural and social sciences literatures on territoriality.

410 Shifting away from implicit linkages to property towards an explicit framework of access also
411 allows animal behaviourists to address the two problems of territoriality identified from the animal
412 behaviour literature. First, the theory of access is designed to focus on what *is* and not *what should be*.
413 As Ribot and Peluso (2003, p. 154) explain by quoting Neale (1998, p. 48—italics in original), a
414 theory of access “retains an empirical “focus on the issues of *who* does (and who does not) get to use
415 *what*, in *what* ways, and *when* (that is, in what circumstances).”” Second, the theory of access is
416 expansive and therefore avoids constraining the possible functions of behaviours and relationships
417 among individuals—“access is about *all* possible means by which a person is able to benefit from
418 things” (Ribot and Peluso 2003, p. 156) and “access analysis is, thus, the process of identifying and
419 mapping the mechanisms by which access is gained, maintained, and controlled” (Ribot and Peluso
420 2003, p. 160).

421 An access-based approach to animal behaviour already has parallels in many conceptions of
422 animal territoriality—see Kaufmann’s (1983) definition of territory above, which focuses on socially
423 determined access, or Waser and Wiley’s (1979, p. 173) proposal “to abandon the search for a
424 unitary definition of territoriality and any simple dichotomy between territorial and nonterritorial
425 species” and instead “address the variation among species in relationships of aggression, isolation,
426 and activity fields, first by considering the behavioural mechanisms that control these

427 relationships...then by considering the selection pressures that can explain their evolution.” But
428 these parallels have thus far been implicit. Without explicitly disambiguating access from property in
429 this context, conceptions of animal territoriality will remain confusing and challenging. An explicitly
430 access-based approach could be integrated with much of the existing literature on animal
431 territoriality as long as animal behaviourists are concurrently careful to examine and clarify the ways
432 in which implicit notions of property have influenced research questions and hypotheses. An access-
433 based lens could also readily integrate research on animal contests, which focuses on individual
434 interactions in light of access to resources (Arnott and Elwood 2009) but may also include
435 embedded notions of ownership (e.g. Hammerstein 1981).

436 Existing research on mating systems can also be incorporated into an access-based
437 framework, which will allow animal behaviourists to be unsurprised by natural variation in mating
438 patterns and will facilitate an important shift away from describing certain mating strategies, such as
439 “sneaker” or “satellite” strategies, as alternatives to a territorial or dominant norm. More radical
440 reconfigurations of mating systems theory, such as Watters’ (2005) co-operator and coercer model,
441 or Kokko and Mappes’ (2013) encounter-based approach to understanding female multiple mating
442 as a null expectation and not an anomaly demanding explanation, fit within an access-based
443 approach as well.

444 **Conclusion**

445 *“Territoriality, after all, is only an abstraction that describes more or less accurately a certain range of*
446 *behaviours that occurs often enough to merit a name.”* (Kaufmann 1983, p. 10).

447 Throughout the history of research on territoriality, animal behaviourists have contended
448 that territoriality is an accurate-enough abstraction for understanding space use, resource use, and

449 mating patterns, but can be resistant to acknowledging its limitations as an explanatory framework.
450 Concurrently, periodic critiques have not yielded a shift away from the hegemonic paradigm of
451 territoriality, possibly because these critiques live squarely within the fields of animal behaviour and
452 behavioural ecology and are thus seen as equivalently valid alternatives to a conception of animal
453 behaviour that centres possession and ownership. By taking past critiques of animal territoriality
454 seriously, and juxtaposing these critiques with literature from the social sciences, we attempt to bring
455 about such a paradigm shift. Specifically, we argue that many past and current conceptions of animal
456 territoriality frequently contain deeply embedded but fundamentally incoherent notions of property,
457 ownership, and authority. We suggest that spatial analyses of social interactions and resource use
458 informed by social scientists' conceptions of access will allow us to reframe how we conceive of
459 animal behaviour in a fuller, more nuanced, and more complex way. We contend that comparable
460 interdisciplinary examinations that meld the natural and social sciences should be a critical part of
461 evaluating whether and how to develop frameworks for understanding any dimension of animal
462 behaviour.

463 **Acknowledgements**

464 We thank Todd Freeburg for pointing us to papers in the animal behaviour literature that
465 sparked this endeavour and Zuleyma Tang-Martinez for encouraging and facilitating the publication
466 of this paper, as well as for her insightful comments on a previous version. For feedback on this
467 paper and the ideas herein, we thank Max Lambert, Ignacio Escalante, Trinity Walls, Maggie Raboin,
468 Malcolm Rosenthal, Damian Elias, Erin Brandt, Yoel Stuart, Nick Herrmann, and two anonymous
469 reviewers. AK is supported by the Miller Institute for Basic Research in Science.

470 **References**

- 471 Ah-King, M. 2007. Sexual selection revisited – Towards a gender-neutral theory and practice.
472 European Journal of Women's Studies 14: 341-348.
- 473 Arnott, G, and RW Elwood. 2009. Assessment of fighting ability in animal contests. Animal
474 Behaviour 77: 991-1004.
- 475 Avise JC, Jones AG, Walker D, DeWoody JA, Dakin B, Fiumera A, Fletcher D, Mackiewicz M,
476 Pearse D, Porter B, and Wilkins SD. 2002. Genetic mating systems and reproductive natural
477 histories of fishes: lessons for ecology and evolution. Annual Review of Genetics 36: 19–45.
- 478 Blomley, N. 2013. Performing Property: Making The World. Canadian Journal of Law &
479 Jurisprudence 26: 23-48.
- 480 Blomley, N. 2016. The territory of property. Progress in Human Geography 40: 593-609.
- 481 Boomsma JJ, Kronauer DJC, Pedersen JS. 2009. The evolution of social insect mating systems. In:
482 Gadaue J, Fretwell J (eds) Organization of insect societies. Harvard University Press,
483 Cambridge, pp 3–25.
- 484 Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of
485 Mammalogy 24: 346-352.
- 486 Bush, JM, and D Simberloff. 2018. A case for anole territoriality. Behavioral Ecology and
487 Sociobiology 72: 111.
- 488 Carpenter, CR. 1958. Territoriality: a review of concepts and problems. In: Roe A, Simpson GG
489 (eds) Behavior and Evolution. Yale University Press, Binghamton pp. 224-250.
- 490 Cockburn, A, L Brouwer, MC Double, N Margraf, and M van de Pol. 2013. Evolutionary origins
491 and persistence of infidelity in *Malurus*: the least faithful birds. Emu 113: 208-217.
- 492 Elgar, MA, Jones, TM, and McNamara KB. 2013. Promiscuous words. Frontiers in Zoology 10: 66.
- 493 Emlen, JT. 1958. Defended area?—a critique of the territory concept and of conventional thinking.
494 Ibis 99: 352.
- 495 Emlen, ST, and LW Oring. 1977. Ecology, sexual selection, and the evolution of mating systems.
496 Science 197: 215–223.
- 497 Fausto-Sterling, A. 1997. Feminism and behavioural evolution: A taxonomy. In: Gowaty, PA (ed)
498 Feminism and evolutionary biology. Chapman and Hall, New York pp. 42-60.
- 499 Gowaty, PA. 1982. Sexual terms in sociobiology: Emotionally evocative and paradoxical jargon.
500 Animal Behaviour 30: 630-631.
- 501 Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific
502 variation and adaptive function. Molecular Ecology 11:2195–2212.

- 503 Gross, MR. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313: 47-48.
- 504 Hammerstein, P. 1981. The role of asymmetries in animal contests. *Animal Behaviour* 29: 193-205.
- 505 Haraway, D. 1989. *Primate visions: Gender race, and nature in the world of modern science.*
506 Chapman and Hall, New York.
- 507 Haraway, D. 1991. *Simians, cyborgs, and women: The reinvention of nature.* Routledge, New York.
- 508 Jones, AG, Walker D, Kvarnemo C, Lindström, and JC Avise. 2001. How cuckoldry can decrease
509 the opportunity for sexual selection: Data and theory from a genetic parentage analysis of
510 the sand goby, *Pomatoschistus minutus*. *Proceedings of the National Academy of Sciences* 98:
511 9151-9156.
- 512 Kamath, A, and JB Losos. 2017. The erratic and contingent progression of research on territoriality:
513 a case study. *Behavioral Ecology and Sociobiology*. 71: 89.
- 514 Kamath, A and JB Losos. 2018a. Reconsidering territoriality is necessary for understanding *Anolis*
515 mating systems. *Behavioral Ecology and Sociobiology* 72: 106.
- 516 Kamath, A and JB Losos. 2018b. Estimating encounter rates as the first step of sexual selection in
517 the lizard *Anolis sagrei*. *Proceedings of the Royal Society B* 286: 20172244.
- 518 Kaufmann, JH. 1983. On the definitions and functions of dominance and territoriality. *Biological*
519 *Reviews*. 58: 1-20.
- 520 Kokko H, and J Mappes. 2013. Multiple mating by females is a natural outcome of a null model of
521 mate encounters. *Entomologia Experimentalis et Applicata* 146, 26–37.
- 522 Lawton, MF, WR Garstka, and JC Hanks. 1997. The mask of theory and the face of nature. In:
523 Gowaty, PA (ed) *Feminism and evolutionary biology*. Chapman and Hall, New York pp. 63-
524 85.
- 525 Linklater, WL. 2000. Adaptive explanation in socio-ecology: lessons from the Equidae. *Biological*
526 *Reviews* 75: 1-20.
- 527 Linklater, WL. 2011. Territorial tuatara? 0 a hypothesis still to be tested. *New Zealand Journal of*
528 *Ecology* 35: 308-311.
- 529 Maine, H.S. 1917. *Ancient Law*. Dutton, Dent.
- 530 Maher, CR, and DF Lott. 1995. Definitions of territoriality used in the study of variation in
531 vertebrate spacing systems. *Animal Behaviour* 49:1581–1597.
- 532 Maher, CR, and Lott, DF. 2000. A review of ecological determinants of territoriality within
533 vertebrate species. *American Midland Naturalist* 143: 1-29.
- 534 Mesnick, SL. 1997. Sexual alliances: evidence and evolutionary implications. In: Gowaty, PA (ed)
535 *Feminism and evolutionary biology*. Chapman and Hall, New York pp. 207-260.

- 536 Neale, WC. 1998. Property: Law, Cotton-pickin' Hands, and Implicit Cultural Imperialism. In: R.C.
537 Hunt, and A. Gilman (eds.) Property in economic context. University Press of America:
538 Monographs in Economic Anthropology, No. 14, Lanham pp. 47-66.
- 539 Noble, GK. 1939. The role of dominance in the life of birds. *Auk* 56: 263-273.
- 540 Orians, GH. 1969. On the evolution of mating systems in birds and mammals. *The American*
541 *Naturalist* 103: 589-603.
- 542 Ostrom, Elinor. 1990. *Governing the Commons. The Evolution of Institutions for Collective Action*. Cambridge
543 University Press, Cambridge.
- 544 Peters, PE. 2010. "Our daughters inherit our land, but our sons use their wives' fields": matrilineal-
545 matrilineal land tenure and the New Land Policy in Malawi. *Journal of Eastern African*
546 *Studies*, 4: 179-199.
- 547 Ribot, JC, and NL Peluso. 2003. A theory of access. *Rural Sociology* 68: 153 – 181.
- 548 Rose, CM. 1985. Possession as the origin of property. *University of Chicago Law Review* 52: 73-88.
- 549 Rose, CM. 1994. Property and Persuasion: Essays on the History, Theory and Rhetoric of
550 Ownership. Westview Press, Boulder.
- 551 Sack, RD. 1983. Human territoriality: A theory. *Annals of the Association of American*
552 *Geographers*. 73: 55-74.
- 553 Stamps, JA. 1994. Territorial behaviour: testing the assumptions. *Advances in the Study of Behavior*
554 23:173–231.
- 555 Strassman, JE, and DC Queller. 2014. Privatization and property in biology. *Animal Behaviour* 92:
556 305-311.
- 557 Taborsky, M. 1994. Sneakers, satellites, and helpers: Parasitic and cooperative behavior in fish
558 reproduction. *Advances in the Study of Behavior* 23: 1-100.
- 559 Tang-Martinez, Z. 1997. The curious courtship of sociobiology and feminism: A case of
560 irreconcilable differences. In: Gowaty, PA (ed) *Feminism and evolutionary biology*.
561 Chapman and Hall, New York pp. 116-150.
- 562 Tang-Martinez, Z. 2014. Animal communication: How and why animals communicate—or do they?
563 In: Yasukawa, K (ed) *Animal behaviour: how and why animals do the things they do*.
564 Praeger, Santa Barbara pp. 51-98.
- 565 Uller T, and Olsson M. 2008. Multiple paternity in reptiles: patterns and processes. *Molecular*
566 *Ecology* 17: 2566–2580
- 567 Walker, P.A. and P. Peters. 2001. Maps, Metaphors and Meanings: Boundary Struggles and Village
568 Forest Use on Private and State Land in Malawi. *Society and Natural Resources* 14: 411–24.

- 569 Waser, P, and RH Wiley. 1979. Mechanisms and Evolution of Spacing in Animals. Social Behavior
570 and Communication. P. Marler and J. G. Vandenberg, Plenum Press, New York: 159-223.
- 571 Watters JV. 2005. Can the alternative male tactics 'fighter' and 'sneaker' be considered 'coercer' and
572 'cooperator' in coho salmon. *Animal Behaviour* 70: 1055-1062.
- 573 Wesner, AB. 2019. Messing Up Mating: queer feminist engagements with animal behaviour science.
574 *Women's Studies: An Interdisciplinary Journal* 48: 309-345.
- 575 Willey, A. (2016). *Undoing Monogamy: The Politics of Science and the Possibilities of Biology*. Duke University
576 Press.
- 577 Zuk, M. 1993. Feminism and the study of animal behaviour. *BioScience* 43: 774-778.