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Skilful mating? Insights from animal contest research

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1 SKILFUL MATING? INSIGHTS FROM ANIMAL CONTEST RESEARCH

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3

4 **Whenever resources are limited and indivisible, fighting will evolve as a means to**
5 **resolve ownership. Among such resources are mates, and individuals (usually**
6 **males) of many species compete agonistically with rivals in order to gain access**
7 **to potential mates. However, securing access is not necessarily enough to**
8 **guarantee a mating nor, if a mating is obtained, to guarantee that it is effective for**
9 **securing reproductive success. Thus in addition to fighting, individuals**
10 **participate in a wealth of behaviours to maximise their reproductive success,**
11 **from courtship to sperm competition to mate guarding. In recent years the**
12 **striking parallels between fighting and mating behaviour have become a subject**
13 **of discussion. In particular, insights have been drawn from the predictions of**
14 **contest theory to help us understand the use of repetitive signalling in courtship.**
15 **Here, we take this discussion further, highlighting similarities between fighting**
16 **and mating in the use of dynamic repeated behaviours, which function to (1)**
17 **advertise quality and (2) convince or coerce an individual to relinquish the**
18 **contested resource (gametes in terms of mating). We focus specifically on a**
19 **performance trait of emerging interest in the field of animal contests, skill. We**
20 **identify behaviours used throughout the mating process in which skill is likely to**
21 **be of importance for securing success, and highlight key questions for future**
22 **study.**

23

24 When fitness depends on access to resources that are indivisible and in limited supply
25 (henceforth limited resources), fighting behaviour will evolve as a means for individuals
26 to secure ownership. Animals fight over many types of limited resources, including food,
27 shelter and territory. When the availability of or access to suitable mates is restricted,
28 their gametes become a limited resource. However, winning a fight is not always
29 necessary to secure access to mates, e.g. alternative tactics used by sneaker males –
30 Engqvist & Taborsky, 2016, and furthermore may not be sufficient to guarantee the
31 victor a mating, particularly when mate choice is involved. Due to the relative costs and
32 benefits of mating with a dominant male, the selection pressures exerted by intra-sexual
33 contests and mate choice are often contrasting (Qvarnström & Forsgren, 1998; Wong &
34 Candolin, 2005), with females of some species exhibiting preferences for losers after
35 eavesdropping on a fight (Ophir & Galef, 2003; Bierbach et al., 2013). Thus, agonistic
36 behaviour can derive from indirect sexual selection in the case of fighting over mates,
37 as well as natural selection in the case of fighting over resources, or via both routes in
38 combination.

39 While fighting and reproduction can be linked due to the former often preceding
40 the latter, there are also direct parallels between the evolution of fighting and
41 reproductive behaviour. This is because individuals trying to access gametes are faced
42 with essentially the same set of problems as individuals fighting over any other limited
43 resource (Mowles & Ord, 2012). Fights occur among two or more individuals with
44 conflicting interests. In order to win a fight, an individual must convince or coerce its
45 opponent to relinquish ownership of the contested resource. Similarly during mating

46 events, individuals adopting one sex role (usually male) must attempt to convince or
 47 coerce individuals adopting a different sex role with divergent interests (usually female)
 48 to grant, preferably exclusive, access to their gametes. Thus, Mowles and Ord (2012)
 49 argued that we should expect to see similar sets of tactics and strategic decision-
 50 making employed in both scenarios: Agonistic signals associated with giving-up
 51 decisions during contests, and courtship signals associated with reproductive decisions
 52 during mating events. Here we expand on this argument to draw parallels between
 53 injurious and sometimes fatal fighting, and coercive/injurious and sometimes fatal
 54 reproductive behaviour (**Table 1**). We then outline how approaches and insights gained
 55 from the study of animal contests should therefore be of value for understanding a
 56 broad range of reproductive behaviours. We give a special focus to the potential
 57 importance of a performance trait of recent interest in the study of animal contest
 58 behaviour, the ability to execute challenging behaviours well, known as *skill*.

59

60 **Table 1** General extended framework for parallels between contest behaviour and
 61 reproductive behaviour

Severity	Trait	Function	Positive outcome in:		Mode of selection	
			<i>Contests</i>	<i>Reproduction</i>	<i>Contests</i>	<i>Reproduction</i>
Low	Signal (potentially involving display of a weapon)	Advertise individual quality	Opponent decides to relinquish resource	Potential mate decides to permit access to gametes	Indirect sexual selection or natural selection	Direct sexual selection
Moderate	Physical strength or	Overpower or	Constrain ability of	Override ability of	Indirect sexual	Direct sexual selection

	weapon	temporarily damage recipient	opponent to continue fighting	potential mate to withhold access to gametes	selection or natural selection	
High	Physical strength or weapon	Reduce lifespan of recipient	Opponent cannot challenge current outcome	Potential mate cannot re-mate with rivals	Indirect sexual selection or natural selection	Direct sexual selection and indirect sexual selection

62

63 **Parallels between contest behaviour and reproductive behaviour**

64 *Signalling*

65 When rivals contest ownership of a limited resource the encounter does not necessarily
66 involve dangerous fighting. Rather, many contests begin with, and may even exclusively
67 consist of, agonistic signals. These signals are typically performed repeatedly, until one
68 of the opponents decides to quit the contest, relinquishing its claim to the resource in
69 question. A great amount of effort has been devoted to understanding the relationships
70 between these repeated signals and the decision of the loser to give up. Briefly, a range
71 of scenarios based on assumptions about the information content of agonistic signals
72 have been formally modelled although not all possible scenarios have been investigated
73 in this way and from those that have, only one has been demonstrated to be a potential
74 evolutionarily stable strategy (see Briffa et al., 2020; Parker, 2019; Leimar, 2019 for a
75 discussion). It is striking that the assumptions underpinning contest theory about what is
76 important to a signal receiver in a contest exactly match our assumptions about what
77 should be important to a signal receiver choosing a potential mate. This is because
78 receivers in both contexts, contests and courtship, are interested in information about

79 the signaler's quality, and signals should evolve to offer reliable indicators of signaler
80 quality (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). Moreover, in both
81 cases this information is used to make a critical fitness decision, to relinquish a limited
82 resource in the case of contest behaviour, or in the case of mate choice to relinquish
83 limited gametes (and, where relevant, to pay the time and energy costs allocated to
84 parental care).

85 If there are parallels in the strategic functions of agonistic and courtship signals
86 then we should expect to see similarities in the tactics that have evolved under similar
87 selective forces. In both cases the agents of selection are the preferences or responses
88 of signal receivers that have an interest in assessing sender quality. Heavily studied and
89 widely known examples of sexual signals involve morphological adaptations typically
90 characterized by striking ornamentation and colouration. Nevertheless, variation in the
91 expression of such traits cannot (on its own) always adequately explain variation in
92 mating success and mate choice operates in many species that lack ornaments entirely
93 (e.g. the majority of mammals) (Byers et al., 2010). Mowles and Ord (2012) suggested
94 that many of the elaborate structures used in courtship signals are actually used in
95 dynamic displays that are performed repeatedly often in a temporally structured way
96 e.g. in bouts of activity separated by pauses (see **Fig 1**), while Byers et al. (2010)
97 proposed that ornaments arise secondarily as a means of enhancing the performance
98 of these displays. Mowles and Ord (2012) concluded that much of the theory used to
99 understand repeated agonistic signals in animal contests should be equally applicable
100 to examples of sexual signals used during courtship. By extension, traits that underpin

101 success in the execution of agonistic signals might be similar to those that underpin
102 successful sexual signals.

103 *Physical combat and restraint*

104 Not all fights are resolved via agonistic signals. When rivals are closely matched,
105 direct force may be used to subdue the opponent, especially if the stakes are high i.e.
106 for a highly prized resource. In fights between shore crabs, *Carcinus maenas*, for
107 example, opponents will use their chelae to perform static displays but also to escalate
108 to more intense tactics such as grappling, striking, pinching and holding their opponent
109 (Sneddon et al., 1997). These fights occur not only to settle ownership of food and
110 shelter but also to establish access to females. Like other crustaceans, female shore
111 crabs are only receptive to sperm for a short window of time after moulting. Therefore,
112 males detect females in a pre-moult state (via kairomone emission, Hardege et al.,
113 2002) and guard them by grasping the female with the chelipeds and walking legs. In
114 this way a male can ensure that he is able to retain exclusive mating access with a
115 receptive female when moulting occurs. During this pre-copulatory mate-guarding
116 another male may attempt to take the female from the guarding male, using the tactics
117 listed above. Moreover, the guarding male must employ similar tactics in order to initiate
118 and maintain guarding of the female regardless of whether other males attempt to
119 dispossess him. This implies that females try to resist guarding, although this has yet to
120 be established. In other species exhibiting pre-copulatory mate guarding, such as water
121 striders *Gerris buenoi* (Watson et al., 1998) and isopods *Thermosphaeroma*
122 *thermophilum* (Jormalainen & Schuster, 1999) pre-copula pairs are clearly in conflict.
123 Females will attempt to remove guarding males, shaking them vigorously, and males

124 must resist this shaking in order to copulate. Thus, while successful fighting can require
125 a rival's agonistic tactics to be countered, the same is true for examples of reproductive
126 behaviour in cases where males must overcome the defensive tactics of females.

127 *Intentional and unintentional injury*

128 Finally, there are examples of fighting in which rivals intentionally injure or even
129 kill their opponent, and wherein differences in the ability to inflict injuries drives variation
130 in fighting success. For example, beadlet sea anemones, *Actinia equina*, injure their
131 opponents by injecting necrotising toxins, and individuals that inflict more injuries win
132 more fights (Rudin & Briffa, 2011). In northern elephant seals, males employ injurious
133 tactics during fights for dominance (and hence enhanced access to females), using their
134 bulk and sometimes their teeth as weapons, biting their rival's head and throat
135 (Sandegren, 1975). Fights between male elephant seals also often result in
136 unintentional injury to females, which occurs when females are subject to copulation
137 attempts by multiple rival subordinates at the harem periphery (Le Boeuf & Mesnick,
138 1990, Mesnick & Le Boeuf, 1991). Similarly, female yellow dung flies can be
139 accidentally drowned in liquid faeces if they are caught up in male-male fights over
140 mate-guarding (e.g. Parker, 1970). In other examples, however, males intentionally
141 injure females during copulation. Male seed weevils, *Callosobruchus maculatus*,
142 possess an aedeagus covered in spines, which pierce the walls of the female genital
143 tract during copulation. This damage appears to increase the fertilisation success of
144 males by providing direct access to gametes and enhanced uptake of seminal fluid
145 (Hotzy et al., 2012). Furthermore, it also enhances the effect of chemicals within the
146 seminal fluid which alter female reproductive physiology (hyperovulation leading to a

147 shortened lifespan) and behaviour (inhibition to remate) in favour of the male (Yamane
148 et al., 2008; Yamane & Miyatake, 2010). Particularly striking examples of intentional
149 damage can be seen in a number of simultaneously hermaphroditic species.
150 Adaptations for reproductive behaviour in such species are thought to be driven by the
151 relative advantage of reproducing in the male sex role compared with the female sex
152 role, leading to conflict over who occupies which role (Scharer et al., 2015). In the
153 Persian carpet flatworm *Psuedobiceros bedfordii*, for example, there is no external
154 opening of the female reproductive system but all individuals possess two
155 pseudopenises on the ventral side of their body. Outcrossing occurs when two
156 individuals engage in frenetic 'penis fencing', twisting around one another, in an attempt
157 to use their everted pseudopenises to deposit streaks of seminal fluid on their mating
158 partner, while avoiding the placement of seminal fluid on their own body. The seminal
159 fluid is acidic and burns through the body wall, allowing sperm to access the female
160 gametes of the recipient. Evidence of the physical cost of losing these encounters
161 includes external scarring and large tears that result in individuals losing most of their
162 body, which they eventually regenerate (Michiels, 1998; Whitfield, 2004).

163 These examples demonstrate functional similarities between behaviours involved
164 in fighting and reproduction which are both characterised by conflict over resource
165 ownership/access, if we include expensive gametes as a resource. While both males
166 and females can benefit from mating, they experience different costs based on their role
167 and level of investment in reproduction which leads to the occurrence of inter-locus
168 sexual conflict (IRSC). Under IRSC the fitness of each sex is optimised under different
169 conditions directly linked to the outcome of their interaction (Schenkel et al., 2018). This

170 sexual conflict results in the sexes holding divergent interests. The extent to which their
171 interests differ, however, will vary across examples (e.g. species, but also at other
172 levels such as life history parameters) depending on the relative costs and benefits of
173 mating, including those associated with injurious mating behaviour as we will discuss
174 later on. Although the interests of fighting rivals are clearly contrasting, the degree of
175 divergence between these interests is also likely to vary across examples, depending in
176 this case on the relative costs of losing. For example, if winning a fight is critical to
177 gaining access to imminently vital resources e.g. safe territory from predators, food in a
178 scarce environment, then the degree of divergence will be high. But if a loser can still
179 gain access to another resource unit, albeit not the optimal one, then the cost of losing
180 and hence the degree of divergence in interests may be lower. Thus while the interests
181 of males and females during mating can be more closely aligned than those of two
182 competitors, the degree of divergence between interests in both contexts is likely to
183 depend on the relative costs and benefits of a particular interaction (Searcy & Nowicki,
184 2005).

185 Therefore, regardless of the mode of selection (sexual or natural, see **Table 1**), we see
186 adaptations that allow individuals to impress, subdue, injure or shorten the lifespan of a
187 recipient, all of which are employed during fighting and mating to gain access to, and
188 secure ownership of, a resource.

189

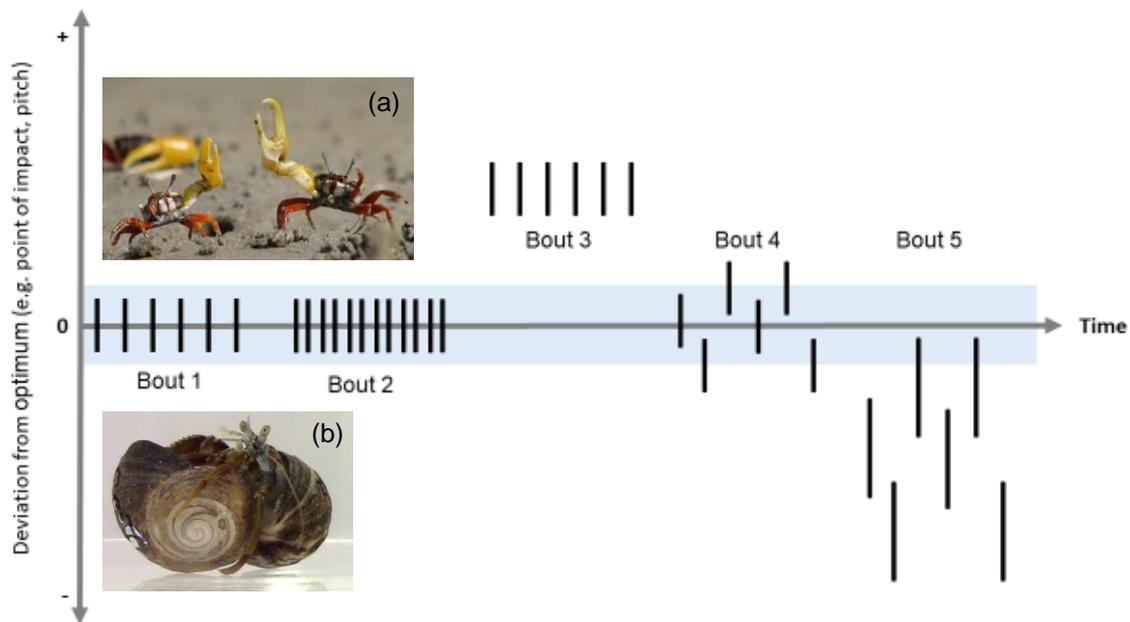
190 **Performance during fights and courtship**

191 If selection has produced similar adaptations for fighting and reproduction, then similar
192 variation in trait values should drive differential success in both contexts. In the case of
193 sexual signals, the expression of striking visual ornaments such as colourful/elaborate
194 plumage in male birds, enlarged chelipeds of male fiddler crabs and colourful dewlaps
195 in reptiles have received much attention (Mowles & Ord, 2012). In many cases the
196 dynamic components of visual signals have also been studied in depth, such as claw
197 waving in fiddler crabs (see Backwell, 2019) and 'push up' or 'bobbing' behaviour in
198 reptiles (e.g. Ord & Evans, 2003). A prominent approach has been to use robotic model
199 animals to mimic and manipulate the temporal pattern of visual courtship signals that
200 are observed, often at distance, by receivers. In contrast, using robots to investigate
201 agonistic signals, which are generally performed at close quarters, if not in direct
202 physical contact, has been less common (however see Qiu et al., 2018 for a recent
203 example). Nevertheless, investigating the dynamic aspects of agonistic signals and
204 other agonistic behaviour has been an area of intense focus in studies of animal
205 contests. This is likely due to a body of contest theory that makes ready predictions,
206 primarily about rates of escalation (see Briffa et al., 2020 for a review). Thus, a typical
207 approach for testing agonistic behaviour has been to stage real fights (i.e. between two
208 real opponents), record the resulting temporal patterns of behaviour, and use these to
209 calculate appropriate metrics of 'vigour' (**Fig. 1**). Often, repeated agonistic behaviours
210 take place in bouts of activity, so measures of vigour might include average number of
211 actions per bout or average duration of pauses between bouts, as in studies of 'shell
212 fighting' in hermit crabs (Briffa, Elwood & Dick, 1998) and 'jump clashing' in fallow deer
213 (Jennings et al., 2005).

214 Analyses of vigour have provided insights into the functions of agonistic
215 behaviour, and variation in vigour has been analysed in relation to contest outcomes as
216 well as to underlying physiological condition (e.g. energy reserves, metabolic by
217 products, hormones - see Briffa & Sneddon, 2007 for a review). However, vigour is not
218 the only aspect of dynamic contest behaviour because rates of performance do not
219 encompass the spatial components of behaviour, which could be important for effective
220 signalling, overpowering or injuring of an opponent. In addition to performing agonistic
221 behaviour at a high rate, recent evidence shows that in fighting and courtship alike it
222 may be equally important to perform the behaviour well, or skilfully (Byers et al., 2010;
223 Barkse et al., 2011). In the next section we explore the idea of skill in more detail and
224 provide examples of how it has been studied in one example of a courtship display and
225 one example of agonistic behaviour. We then go on to review a range of reproductive
226 behaviours, from courtship displays through to coercive matings, in which interacting in
227 a skilful way may contribute to reproductive success.

228

229



230

231 **Figure 1.** Illustration of vigour (rate and magnitude) and skill for repeated challenging
 232 activities such as a claw waving displays in male fiddler crabs (a; *Austruca mjoebergi* -
 233 credit: Patricia Backwell) and agonistic shell rapping behaviour in fighting hermit crabs
 234 (b; *Pagurus bernhardus* – credit: Sarah Lane). The x-axis represents time and the y-axis
 235 represents deviation from an optimal performance, black vertical lines denote single
 236 instances of a behaviour within a sequence (e.g. a strike, an appendage wave or a song
 237 note) and line height represents the magnitude of the behaviour. The blue area
 238 represents the zone around that optimum where actions have their strongest effect on a
 239 recipient of the signal or direct action. Some potential examples of deviation are; spatial
 240 deviation in points of impact away from the most effective place to strike an opponent in
 241 a fight, spatial deviation from the optimal movement path for a visual display such as
 242 claw waving in fiddler crabs or acoustic deviation from the optimal pitch of a vocal call.
 243 Compared to bout 1, bout 2 is more vigorous in terms of rate of performance as it

244 contains more actions per unit; bout 3 has the same temporal vigour but is less
245 accurate; bout 4 has the same temporal vigour and accuracy but is less precise; bout 5
246 lacks accuracy and precision but contains actions of greater magnitude, such as power
247 of impact or sound intensity. Bout 5 might also be inefficient if the magnitude exceeds
248 that which is required for a positive outcome.

249

250 **Skill**

251 *Definition of skill*

252 Skill, defined as performing a challenging behaviour well, captures the quality of
253 behaviour rather than the vigour (Byers et al., 2010). Although the term 'quality' has
254 been used in various contexts e.g. the quality of a male from the perspective of a
255 female, here we use it to refer to the quality of motor patterns with which behaviours are
256 performed. This type of quality can be quantified by a wide range of parameters across
257 different contexts, and by multiple parameters even within a single example. Briffa and
258 Lane (2017) defined four general parameters that are pertinent to skill in dyadic combat.
259 Our aim in this previous paper was to identify skill-related aspects of agonistic
260 behaviour that could be meaningfully applied across diverse study species in the same
261 way that the concept of vigour is broadly applicable. The first parameter is *efficiency*, in
262 which behaviours are performed with the optimal amount of effort in terms of balancing
263 the investment in energy against (a) the intended effect on the opponent and (b) other
264 requirements such as maintaining high vigour. Second, we defined *accuracy* as the
265 degree of congruence between the motor pattern required for maximum effect and what

266 is actually performed (**Fig. 1**). Third, we defined *precision* as the degree of variation
267 around efficient and accurate actions (**Fig. 1**). This parameter corresponds to the idea
268 of behavioral consistency or intra-individual variation (Stamps et al., 2012; Westneat et
269 al., 2015), a component of animal personality. While precision could ensure that an
270 optimal target area is repeatedly struck in a fight (Lane & Briffa, 2020), it has also been
271 suggested that consistency of signaling behaviour may be under direct sexual selection
272 (Schuett et al., 2010).

273 If vigour captures the temporal component of repeated agonistic behaviour, then
274 these first three components of skill (efficiency, accuracy and precision) capture its
275 spatial performance. Our final component of fighting skill, *appropriateness*, concerns the
276 effectiveness of decision-making during combat. Appropriateness is defined as the
277 degree to which the optimal tactic is chosen from a range of possible tactics that could
278 be deployed at different points during a fight. All of these definitions of skill apply to
279 direct combat where one contestant could interfere with the other's ability to execute
280 agonistic behaviour. If there is no direct contact these parameters could be more
281 narrowly defined as capturing 'technique', which we define as the ability to carry out
282 challenging behaviours well in the absence of potential interference. A similar distinction
283 could be appropriate for reproductive behaviours where the recipient of a signal may
284 have no obvious influence on the capacity of the sender to perform it, whereas in the
285 case of coercive reproduction a resisting female (for example) might directly impair the
286 ability of a male to perform activities such as mate guarding with efficiency, accuracy
287 and precision. Since technique and skill are both described by the same parameters,
288 however, we will use the term skill to refer to both. In the next section we briefly review

289 the current evidence for the role of skill during animal contests. These aspects of skill
 290 thus attempt to capture the quality of performances, in contrast to other aspects of
 291 performance (vigour, i.e. the rate and magnitude) that are typically analysed in studies
 292 of animal signalling and other dyadic interactions (**Table 2**). As described below,
 293 however, for a given example of animal performance, there may be correlations among
 294 the different components of performance, which complicates the task of deciding
 295 whether a measure is best described as a component of vigour, magnitude or skill.

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301 **Table 2** Distinction between different animal performance traits used in contests and
 302 reproduction (illustrated in Fig. 1) with examples of potential measures.

Aspect	Vigour		Technique/Skill
Definition	Rate of performance	Magnitude of performance	Quality of performance
Example parameters	<ul style="list-style-type: none"> - No. of actions per bout - Intra-bout interval between actions - Inter-bout interval 	<ul style="list-style-type: none"> - Sound intensity - Force of impact - Size of display 	<ul style="list-style-type: none"> - Efficiency - Accuracy - Precision - Appropriateness
Example	Number of raps per	Power of impact of	Hermit crab shell rapping: -

measures (contests)	bout in fighting hermit crabs (Briffa et al., 1998).	individual raps in fighting hermit crabs (Briffa et al., 2003).	Displacement distance (Briffa & Fortescue, 2017); mean and variance in point of impact of raps (Lane & Briffa, 2020); change from shell rapping to rocking (Edmonds & Briffa, 2016).
Example measures (reproduction)	Number of waves per minute in male fiddler crabs (Backwell et al., 1999).	Sound intensity of calling in male anurans (Tanner & Bee, 2020) or birds (Leedale et al., 2015).	Postures of limbs during dancing in humans Neave et al., (2010); decision to fire a love dart in snails (Chase & Blanchard, 2006).

303

304

305 *Skilful fighting*

306 Hermit crabs fight over the occupancy of empty gastropod shells which they rely on for
 307 protection. Most fights are initiated by an attacking crab in a shell that is too small
 308 against a defending crab in a shell that would provide the attacker with a better fit. Since
 309 both males and females require shells, both sexes engage in these fights and the two
 310 roles (attacker and defender) are not sex-dependent (Briffa & Dallaway, 2007). The
 311 attacker initiates the fight by grasping the defender that remains withdrawn into its shell.
 312 The attacker then proceeds to perform shell rapping, wherein it strikes its own shell
 313 repeatedly against that of the defender. If the attacker raps with sufficient vigour (i.e.
 314 rate of rapping) (Briffa et al., 1998) and magnitude (i.e. power of impacts) (Briffa et al.,
 315 2003), the attacker is typically able to evict the defender from the contested shell,
 316 pulling it out through the aperture. Recent analyses have shown that spatial

317 components of shell rapping, as well as the various temporal measures enhance the
318 chance of eviction (see Briffa, et al., 1998; Briffa et al., 2003; Briffa & Elwood, 2000b for
319 detailed descriptions). Fortescue and Briffa (2017) measured the displacement distance
320 of raps and found that attackers that displaced by lower distances (i.e. rapped more
321 efficiently) were more likely to elicit an eviction, possibly because efficient rapping is
322 associated with high vigour, i.e. those that displaced by lower distances rapped at a
323 greater rate. This leads to the possibility that efficiency could facilitate sustained vigour
324 through enhanced energy conservation. Although the possibility has yet to be
325 investigated, it seems feasible that different components of skill and vigour might also
326 be associated via trade-offs. For example, a high rate of activity might be traded off
327 against magnitude, or precision might be sacrificed in favour of rate or magnitude.

328 Understanding the causality of any associations between different components of
329 skill or vigour is a challenge, because ideally it would require manipulation of at least
330 one component. Possibilities include manipulation of energetic state in the case of
331 vigour and introduction of physical constraints that would restrict the range of movement
332 in the case of skill. Insight may also be gained from observing changes in vigour and
333 skill as interactions progress. In the case of shell rapping, Fortescue and Briffa (2017)
334 found that as fights progress, displacement distances increase and vigour decreases,
335 suggesting that the effects of fatigue lead to a decline in both skill and vigour. This effect
336 was more marked in losers than winners, with the overall pattern of effective fighting
337 decreasing as the contest proceeds bearing striking similarity to that found in a study of
338 Egyptian three-bout boxing (El Ashker, 2011) - the only other study of within-contest
339 changes in skill of which we are aware.

340 In addition to efficiency, the three other aspects of skill have also been
341 investigated in hermit crab shell fights. Lane and Briffa (2020) found that attackers that
342 could accurately hit a specific zone on the defender's shell were more likely to succeed
343 than those that missed this zone, possibly because of direct effects on the abdominal
344 musculature of defenders. However, fine-scale variation within this zone was not
345 associated with victory, indicating that precision is less important than overall accuracy.
346 Finally, Edmonds and Briffa (2016) demonstrated that when attackers were
347 experimentally prevented from rapping effectively, the attacking crab switched to a less
348 vigorous activity of shell rocking, which seems more appropriate when rapping is less
349 effective.

350 While each of the four suggested parameters of skill have been investigated in
351 hermit crab fights, as discussed in Briffa and Lane (2017), these parameters should be
352 relevant to contests more generally, and furthermore to conflict outside of contests per
353 se. In the section below we consider how the four parameters of skill could be applied to
354 the performance of reproductive behaviour.

355

356 **Reproductive skill?**

357 As we have already discussed, fighting often precedes mating, so skilful fighting could
358 enhance reproductive success (greater rates of copulation and insemination) if agonistic
359 victory leads to increased access to mates. Alternatively, skilful fighting could increase
360 reproductive success if it reliably advertises individual quality to potential mates. Indeed
361 it has been suggested that because motor performance reflects whole-organism

362 performance, it provides a more reliable indicator of genetic quality than elaborate but
363 static ornaments (Byers et al., 2010). Furthermore, motor performance will provide a
364 more up-to-date picture of signaller quality, which may have deteriorated or improved
365 since the production of the static ornament. In pronghorn, *Antilocapra americana*, for
366 example, females observe male-male fights, sometimes even inciting them, and appear
367 to mate preferentially with males that fight more vigorously (Byers et al., 1994; Byers et
368 al., 2010). If females can utilise the vigour with which a male fights as an indicator of his
369 underlying quality, it is also then possible that how skilfully a male fights could provide
370 females with similar information as they seek a high quality mate. It has even been
371 suggested that skill may be a more valuable indicator of quality, reflecting not only
372 current health but also the developmental stability of an individual's musculoskeletal,
373 nervous and sensory systems (Byers et al., 2010). Thus dynamic displays in both
374 fighting and courtship may provide females with a whole host of information garnered
375 from the vigour and skill with which they are performed. If this is the case, and if females
376 are able to utilise this information, we should expect to see a direct link between
377 variation in skill and variation in reproductive success. In the following section, we
378 review the available evidence for the role of reproductive skill, and consider examples of
379 reproductive behaviour where a role for skill is strongly implied (**Table 3**).

380

381 *Courtship displays*

382 As in other animals, humans perform repetitive courtship displays, which is one of the
383 functions of dancing. As in the example of fighting hermit crabs, both vigour and skill

384 seem to be important for success. In their analysis of female perceptions of male dance
385 quality, Neave et al. (2010) demonstrated that female observers prefer men who move
386 their right knee rapidly, over men who move this body part more slowly. Furthermore,
387 women were more interested in men who moved their neck and trunk with consistent
388 displacement distances. A similar capacity for female visual discrimination of slight
389 differences in dance patterns has been shown in golden-collared manakins *Manacus*
390 *vitellinus*. Female *M. vitellinus* exhibited discrimination between male performances on
391 the order of tens to hundreds of milliseconds, with females showing preferences for
392 males who were a fraction of a second faster at certain moves (Barske et al., 2011). In
393 semi-terrestrial fiddler crabs, males have asymmetrically sized chelipeds and wave their
394 large cheliped during intra-sexual contests over territories and in displays used to attract
395 receptive females to their burrows. Fiddler crabs typically inhabit intertidal flats at high
396 population densities, and experiments with robotic crab models show that females
397 prefer males that wave first among many waving males in a given location (Reaney et
398 al., 2008). Males seem to attend to the waving activity of others, rapidly executing a
399 wave once another male initiates waving, indicating that the males must make decisions
400 about appropriate timing of waving. In addition to precedence, females show
401 preferences for certain wave characteristics. Males that wave vigorously are more
402 successful than those that perform more slowly (Backwell et al., 1999) and the
403 amplitude of waving is also important (Jordão et al., 2007). Observations of male fiddler
404 crabs (e.g. see online videos associated with studies such as Reaney et al., 2008; or
405 Mowles et al., 2017) illustrate that the wave patterns themselves occur in three
406 dimensions. Typically there seems to be an elliptical component, a specific direction of

407 movement around that elliptical path, and a specific part of the wave when the ellipse is
408 performed; rather than a simple 'up and down wave'. Perhaps, in addition to variation in
409 vigour, there is also the potential for variation among males in the accuracy and
410 precision of their claw motion paths during a wave, in comparison to an optimal motion
411 path that females will find maximally attractive. An alternative explanation is that these
412 wave paths might simply represent mechanical constraints on claw movement. These
413 possibilities could be investigated using robot fiddler crabs, an approach which has
414 been highly successful in investigating the effects of waving vigour and synchrony within
415 populations of fiddler crabs (review by Backwell, 2019).

416 Spatial components of male courtship displays were also analysed in Manica et
417 al.'s (2017) study on blue-black grassquits, *Volatinia jacarina*. Males of this species
418 perform a multicomponent courtship display, which involves leaping vertically off a
419 perch, hovering at the top of the leap and dipping forwards (so the head is facing down),
420 recovering the original orientation and then returning to the perch, all while performing a
421 vocal signal. Four parameters of these displays; leap height, duration, launch velocity
422 and number of wing beats correlated positively with one another, and with vigour (i.e.
423 the rate of leap displaying). Of these, the number of wingbeats seems to equate to the
424 rate component of vigour, while leap duration and launch velocity seem to equate to
425 measures of magnitude. Leap height may also equate to magnitude (if higher leaps are
426 more attractive to females) or, alternatively, to efficiency (i.e. higher leaps are not more
427 attractive and represent wasted effort). In this case, the result is the opposite of that
428 gained by Fortescue and Briffa (2015) who found a negative association in hermit crabs
429 between displacement distance (i.e. the inverse of efficiency) and vigour. Perhaps then,

430 the correct way to interpret the *V. jacarina* data is that high leap height does not
431 represent low efficiency but instead provides another positive measure of performance,
432 which may be important to female signal receivers. In contrast, rotation angle seems
433 more convincing as a parameter of skill. Rotation angle varies markedly across
434 individuals and correlates less strongly with vigour and the other spatial parameters
435 described above. The question of whether variation in dip angle predicts female
436 preferences for males therefore warrants further investigation.

437 While the majority of courtship displays involve uni-directional signaling from one
438 individual to another, some displays require coordinated behaviour among two or more
439 individuals. This can either be between suitors, as in the duets of long-tailed manakins
440 *Chiroxiphia linearis* in which males perform courtship songs and dances together
441 (Trainer et al.,2002), or between the male and female themselves as in the pair-
442 formation “ceremonies” of the western grebe *Aechmophorus occidentalis* (Nuechterlein
443 & Storer, 1982). In bearded manakins *Manacus sp.*, males begin their acrobatic
444 courtship display alone, but an interested female will then join in, after which the male
445 paces his movement patterns to her behaviour, seemingly allowing her to “lead” the
446 dance (Barske et al., 2015). Although skill has not been investigated in such examples
447 under the framework laid out by Briffa and Lane (2017), it is clear that these coordinated
448 performances require a high level of motor control and thus are candidates for further
449 research into mating skill.

450

451 *Acoustic signals*

452 In many species both contests and courtship involve acoustic signalling as well as the
453 visual displays discussed thus far. Anurans offer a well-known example of this, and
454 performance parameters such as rate (vigour) and amplitude (magnitude) of calling
455 have been studied in depth (see Tanner & Bee, 2020). Furthermore, anurans vary the
456 pitch of their calling in response to conspecifics (Tanner & Bee, 2019) and background
457 noise (Vélez & Bee, 2013). This ability could be analogous to the spatial parameters of
458 skill (Briffa & Lane, 2017) since varying pitch involves the coordination of the vocal
459 apparatus. Furthermore, changing pitch also requires deciding on the most appropriate
460 type of call to give under temporal and spatial variation in sound landscapes. Vocal
461 repertoires have been described in detail for some anurans, for example the olive frog
462 *Babina adenopleura* (Chaung et al., 2016), so there is good scope for formally
463 investigating the role of skill in anuran vocalisations.

464 Acoustic signal variation is heavily studied in birds. Song characteristics can vary
465 with capacities for muscular coordination both of the vocal apparatus itself (e.g. aperture
466 dilation in zebra finches; Williams, 2001) and of general body movements (e.g. in
467 canaries; Suthers et al., 2012). Given that birdsong may also be performed in
468 conjunction with visual display movements, singing may encode information on overall
469 capacities for coordinated control of the vocal apparatus and general musculature
470 (Nuechterlein & Storer, 1982; Dalziell et al., 2013; Hoepfner & Goller, 2013; Manica et
471 al., 2017). Birdsong clearly varies in terms of vigour (e.g. number of trills per song
472 element, repetition rate of song elements) and magnitude (sound intensity) (e.g.
473 Leedale et al., 2015). Birds also show intra-sexual variation in other song parameters
474 that might represent skill, such as pitch and song complexity. Pitch will be constrained

475 by neuromuscular coordination of vocal apparatus (Suthers et al., 1999), and complexity
476 by experience and cognitive ability (Searcy & Nowicki, 2019), although cognitive ability
477 does not necessarily vary with song complexity in the expected direction (Anderson et
478 al., 2017). Many birds also have the capacity to mimic song, displaying extreme vocal
479 complexity produced by controlled manipulation of the vocal muscles (Zollinger &
480 Suthers, 2004) and evidence suggests that females prefer males that produce the most
481 accurate imitations (Zann & Dunstan, 2008). Furthermore, both potential features of skill
482 will also be constrained by morphology and energetic costs (Oberweger & Goller, 2001;
483 Goller, 2021), again highlighting the potential for correlations among vigour, magnitude
484 and skill. Although such inter-relations will present challenges in terms of disentangling
485 the effects of different vigour and skill traits (see Questions 2-4 in the final section),
486 there nevertheless appear to be several features of bird song that could be usefully
487 analysed within the framework proposed for skill.

488

489 *Mate guarding*

490 As discussed above, there are many examples of pre-copulatory mate guarding in
491 which males hold onto females and thus attempt to retain exclusive mating access.
492 Analysis of such pairs typically shows evidence of size-assortative mate guarding,
493 which results from male-male contests over guarded females (e.g. amphipods - Prenter
494 et al., 2006) and from female resistance to guarding, whereby males that are small
495 relative to the female are more likely to be thrown off (e.g. isopods - Jormalainen &
496 Schuster, 1999, and insects; Watson et al., 1998). If body size is heritable, both

497 scenarios could benefit females because they will eventually mate with larger males that
498 produce larger (and potentially fitter) offspring. But bulk may not be the only determinant
499 of successful mate guarding. Firstly, if females resist then male success may depend on
500 how skilfully they are able to grapple, which typically involves coordinated muscle
501 movements requiring efficiency, accuracy and potentially precision if there are repeated
502 bouts of grappling. Secondly, rapid decision-making may be required to choose
503 appropriate grappling tactics to counter female resistance. In some species, males must
504 align specific parts of appendages to compatible regions on the female's body, and in
505 these cases accuracy (and precision if the grip must be repeatedly established) should
506 be important. In one such case, some isopods males bear minute projections on the
507 inner surfaces of their rear gnathopods, which correspond to specific depressions in the
508 cuticle of females (Hume et al., 2005). Similarly, in male diving beetles *Agabus*
509 *uliginosis*, the walking appendages are covered in suckers for grasping females, but
510 these can only form an effective vacuum if applied to particular sections of the female's
511 elytra that lack longitudinal ridges (Bilton et al., 2016).

512 *Coercive mating*

513 Mate guarding restricts the options available to guarded individuals prior to and
514 following copulation, but the successful transfer of gametes may also involve coercive
515 behaviours other than guarding. As we have already seen, simultaneous
516 hermaphrodites such as *P. bedfordii* may benefit more from adopting the male sex role
517 rather than the female sex role, and therefore attempt to donate rather than receive
518 sperm during pre-mating battles. In *P. bedfordii*, timing the release of seminal fluid onto
519 an opponent at an appropriate moment (i.e. when the risk of receiving sperm from the

520 opponent is minimised) could be important. A similar form of traumatic insemination
521 occurs in the orange stripe flatworm, *Pseudoceros bifurcus*. In this case, each individual
522 tries to ensure that it donates rather than receives sperm by stabbing its penis through
523 the opponent's epithelium to allow for hypodermic injection of seminal fluid (Schärer,
524 Janicke & Ramm, 2015). As well as relying on appropriate timing, success could also
525 depend on accuracy if targeting a specific body part increases the chance of
526 insemination while minimising the risk of receiving sperm and incurring an injury. A
527 particularly striking example of the importance of accuracy in simultaneous
528 hermaphrodites is the use of 'love darts' in helcid land snails such as the garden snail
529 *Helix aspersa* (Whitfield, 2004). These are relatively large calcareous spines that are
530 fired from the penis of one mating partner into the visceral mass, head or foot of the
531 other, during a courtship dance prior to sperm transfer. Successfully firing a dart into the
532 partner increases the paternity of the 'shooter' (Chase & Blanchard, 2006), while there
533 appear to be no benefits of being shot for the recipient (Chase, 2007). Therefore, firing
534 the dart at an appropriate time appears to be important. Accuracy may also be key, as a
535 substantial proportion of darts fail to penetrate or pass through the intended recipient
536 entirely. Presumably, inaccurate shots not only result in a waste of resources but may
537 also reduce the delivery of the chemical payload, contained in the shooter's mucus
538 which coats the dart, which contributes to the effect of enhanced paternity (Chase &
539 Blanchard, 2006).

540 The accuracy of sperm deposition may also be an important determinant of
541 insemination success in dioecious species, in particular those that employ traumatic
542 insemination. Male bed bugs, *Cimex sp.*, pierce their intromittent organ through the

543 female cuticle in order to inject ejaculates. Females have evolved a specialised organ,
544 the spermalege, as a means to reduce the costs of traumatic insemination (Morrow &
545 Arnqvist, 2003). Indeed evidence indicates that if males miss the spermalege and inject
546 sperm elsewhere, the damage not only leaves females susceptible to infection, but also
547 reduces fertilisation success, thus affecting the fitness of both parties (Davis, 1965;
548 Reinhardt et al., 2003; Kamimura et al., 2014). In giant squid, *Architeuthis dux*, males
549 inject spermatophores, possibly under hydraulic pressure, through the epithelium and
550 into the arms of females. Again, a need for accuracy is implied in this species, if, as in
551 the bed bugs, the male must penetrate a specific body part of the female for successful
552 fertilisation. Furthermore, male squid may vary in their ability to choose appropriate
553 behaviour, with both male and subadult female specimens having been reported
554 bearing injected spermatophores (although females may be capable of long term sperm
555 storage) (Normal & Lu, 1997).

556

557

558 **Table 3** Examples of contest and reproductive behaviour in which the importance of skill has either been studied or is

559 strongly implied.

	Information transfer				Direct effects			
	Species	Behaviour	Skill studied?	References	Species	Behaviour	Skill studied?	References
Contests	European hermit crabs, <i>Pagurus bernhardus</i>	Attackers rap shell repeatedly against defender.	Y - efficiency (displacement distance), appropriateness, accuracy and precision (distribution of raps)	Briffa & Fortescue, 2017; Edmonds & Briffa, 2016; Lane & Briffa, 2020	European hermit crabs, <i>Pagurus bernhardus</i>	Attackers rap shell repeatedly against defender.	Y - efficiency (displacement distance), appropriateness, accuracy and precision (distribution of raps)	Briffa & Fortescue, 2017; Edmonds & Briffa, 2016; Lane & Briffa, 2020
	Broad-horned flour beetles, <i>Gnathocerus cornutus</i>	Same-sex sexual behaviour to assert dominance without escalation to fight	N - appropriateness implied, decision to switch roles	Lane et al, 2016	Humans, <i>Homo sapiens</i>	Boxing - on target punches.	Y - accuracy and precision	Ashker, 2011
	Cuttlefish, <i>Sepia officinalis</i>	Males adopt different tactics (aggressive or deceptive).	N - appropriateness implied, switch tactics in response to challenger size	van Staaden et al, 2011	Mantis shrimp, <i>Neogonodactylus bredini</i>	Telson sparring	N - but accuracy implied (reduced risk of damage by striking onto telson)	Green & Patek, 2015
	Downy woodpeckers, <i>Dryobates pubescens</i>	Drumming displays	N - but motor skill implied	Schuppe & Fuxjagger, 2017	Richardson's ground squirrels, <i>Spermophilus richardsonii</i>	Lateral swerving	N - but motor skill implied	Pellis et al, 1996
Reproduction	Blue-black grassquits, <i>Volatinia jacarina</i>	Courtship leap display	Y - Accuracy and precision	Manica et al, 2017	Persian carpet flatworms, <i>Pseudobiceros bedfordi</i>	Penis fencing	N - accuracy implied	Michiels, 1998; Whitfield, 2004
	Long-tailed manakins, <i>Chiroxiphia linearis</i>	Males coordinate to perform courtship songs together	Indirectly - accuracy and precision. Song variability and frequency-matching get better with age	Trainer et al, 2002	Garden snail, <i>Helix aspersa</i>	Shoot 'love darts' at one another in order to fertilise	N - accuracy implied. Individuals that miss take longer to copulate after dart shooting begins	Adamo & Chase, 1988; Rogers & Chase, 2001
	Zebra finches, <i>Taeniopygia guttata</i>	Courtship song	Indirectly - song characteristics associated with different beak movements	Williams, 2001	Bed bugs, <i>Cimex</i> sp.	Traumatic insemination into spermalege	N - accuracy implied. Location of insemination directly affects fertilisation success and female longevity	Davis, 1965; Reinhardt et al, 2003; Kamimura et al, 2014
	Superb lyre birds, <i>Menura novaehollandiae</i>	Courtship dances coordinated with songs	N - but motor skill implied	Dalziel et al, 2013	Giant squid, <i>Architeuthis</i> sp.	Males inject spermatophores into female tentacles	N - accuracy and appropriateness implied, injecting females in right place, avoiding injecting males or themselves	Norman & Lu, 1997
	Brown-headed cowbirds, <i>Molothrus ater</i>	Courtship - visual displays coordinated with songs	N - but reliance on capability for fine motor coordination implied	Hoepfner & Goller, 2013	False garden mantis, <i>Pseudomantis albobimbrata</i>	Cannibalism avoidance (approaching females)	N - appropriateness implied. Knowing when to approach, adapting speed of approach to avoid detection	Barry et al, 2009
	Fiddler crabs, <i>Afruca tangeri</i>	Waving displays	N - but find variation in spatial component of wave "maximum altitude"	Jordao et al, 2007	Golden orb spider, <i>Nephila fenestrata</i>	Opportunistic mating with feeding females to avoid cannibalism	N - appropriateness implied.	Fromhage & Schneider, 2004
	Proghorns, <i>Antilocapra americana</i>	Circle chase - male chases female in tight circles	N - but possible signal of ability and agility	Byers et al, 2010	Giant Australian cuttlefish, <i>Sepia apama</i>	Rapid transient sexual mimicry (including posture of arms)	N - motor skill implied to gain correct position for rapid insemination whilst fooling rival	Hanlon et al, 2005
	Western grebes, <i>Aechmophorus occidentalis</i>	Elaborate coordinated courtship displays between males and females	N - accuracy and precision implied for successful coordination	Nuechterlein & Storer, 1982	Diving beetles, <i>Agabus uliginosis</i>	Male appendages covered in suckers for grasping females	N - accuracy implied as suckers only effective on certain parts of females' elytra	Bilton et al, 2016

560 **Selection for skill**

561 Since males and females are in inter-locus sexual conflict (Schenkel et al., 2018), it is
562 not surprising that there are similarities and indeed overlap between adaptations used in
563 reproductive and contest behaviour. Contest behaviour, especially in males, can result
564 from indirect sexual selection when it grants enhanced access to mates. Furthermore,
565 when females preferentially mate with males based on their performance during a fight
566 (e.g. pronghorn - Byers et al., 2010; elephant seals – Cox, 1981), direct sexual selection
567 may also contribute to the evolution of contest behaviour. Finally, as animals fight over
568 resources other than mates (and in some cases males and females compete over the
569 same resources), agonistic traits, including skill, can also be explained by natural
570 selection (**Table 1**).

571 Regardless of the mode of selection, similar performance components should be
572 selected for with regards to skill in contests and reproduction. Spatial components of
573 skill including accuracy, precision and efficiency require the same underlying traits of
574 controlled and coordinated movement patterns, regardless of the specific behaviour
575 being expressed. These components of skill will be selected for whenever spatial skill is
576 important for securing success, be it convincing an opponent to retreat, matching the
577 preferences of choosy potential mates, or guarding, coercing or damaging mates in
578 order to maximise reproductive success. As both mating and contests represent social
579 interactions, skilful behaviour in these contexts will also entail the ability to rapidly deal
580 with countermeasures made by the opponent or potential mate and to choose the
581 appropriate course of action from a range of tactics. In contests this reactive aspect of

582 skill may be important for both opponents regardless of the role each plays (e.g.
583 attacker or defender etc) and similarly in mating events, being able to respond quickly to
584 the behaviour of a potential mate will be important for both males and females,
585 especially in cases when sexual conflict is substantial (e.g. coercive mating, traumatic
586 insemination). While above we have discussed the potential importance of skill for the
587 individual (usually the male) conducting the mate guarding or coercive mating, skill may
588 also be important for the successful resistance of these behaviours by females. Overall,
589 selection for traits that produce skilful behaviour should favour well-coordinated neuro-
590 muscular systems coupled with cognitive abilities that allow rapid decision making, both
591 on the scale of continuous adjustment to counter the activities of a rival or potential
592 mate (e.g. a male water strider being able to resist the female's attempts to shake him
593 off), or to choose the most appropriate action from a range of alternatives (e.g. the
594 decision of a female water strider to engage in energetically costly shaking or not,
595 driven by the harassment rate - Watson, Arnqvist & Stallmann, 1998). In conjunction
596 with underlying physiological systems, learning appears to play a key role in the
597 development of skilful fighting behaviour e.g. via play fighting (see Byers & Walker,
598 1995), and may also be important for the development of reproductive skill. Indeed,
599 differences in the capacity for learning could play a role in explaining variation in
600 reproductive skill. Finally, the relative contributions of genes and social environment,
601 and their potential interaction (i.e. G x G) to skilful behaviour have yet to be addressed
602 and form one of the key questions that we have identified in the following section.

603

604 **Conclusion and future directions**

605 The role of skill in fighting - performing a challenging behaviour well when faced with a
606 real opponent - has thus far only been addressed in a handful of studies (Byers et al.,
607 2010; Edmonds & Briffa, 2016; Green & Patek, 2015; Briffa & Fortescue, 2017; Lane &
608 Briffa, 2020). In terms of reproductive behaviour, there have been even fewer studies in
609 which skilful performance of reproductive signals has been investigated (e.g. Barske et
610 al., 2011; Manica et al., 2017). Given the elaborate nature of many courtship displays,
611 there are a vast number of study systems that could be amenable to investigation
612 (**Table 3**). Furthermore, as discussed earlier, analyses of the vigour of courtship
613 displays are also relatively rare (Mowles & Ord, 2012) so there is a clear opportunity to
614 study temporal (vigour) and spatial (skill) components simultaneously, as has been the
615 case in recent studies of fighting skill (Briffa & Fortescue, 2017; Lane & Briffa, 2020).
616 We now outline four questions that we consider priorities in order to determine whether
617 reproductive skill is important for reproductive success:

618 **Question 1: Does skill predict outcomes?** This question is fundamental to
619 understanding the adaptive value of skill - if reproductive skill is an adaptive trait then
620 skilled individuals should have enhanced mating success (i.e. greater rates of
621 copulation and insemination). Testing this possibility requires experiments in which skill
622 is used as a predictor of outcomes, an approach which is frequently used in studies of
623 fighting behaviour. In hermit crabs, for example, measures of skill relating to accuracy,
624 precision (Lane & Briffa, 2020) and efficiency (Briffa & Fortescue, 2017) have been
625 obtained from freely interacting individuals and used as predictors of victory. In studies
626 of reproductive signals a different approach of artificially manipulated signals is often
627 used to investigate performance traits. For example, robotic models have been used to

628 assess female preferences for male visual display components in lizards (Clark et al,
629 2015), birds (Catchpole & Slater, 1995) and anurans (e.g. Robertson, 1986), while
630 manipulated playback experiments have been used to probe female preferences for
631 components of acoustic signals (e.g. Gerhardt, 1991; Drăgănoiu et al., 2002; Marquez
632 et al., 2008). However, investigations of reproductive signals using naturally interacting
633 animals should also be possible. In fiddler crabs (Jordao et al., 2007) and birds (Manica
634 et al., 2017), variation in specific spatial components of male visual displays have been
635 quantified, and such measures could presumably be used as predictors of female
636 preferences and mating success.

637 **Question 2: If skill does predict outcomes, why?** In fighting, agonistic behaviours
638 can enhance the chance of victory because (1) they provide opponents with information,
639 (2) they exert direct effects on the opponent or (3) a combination of both reasons. As we
640 have argued above, reproductive behaviour can be thought of in similar ways, whereby
641 success can be enhanced through both advertisement and direct action. If reproductive
642 skill predicts outcomes then a key question is whether this is because skilled individuals
643 are more attractive to potential mates or because skill allows greater access to mates
644 (e.g. in pronghorn, Byers et al., 2010), better defence of mates, or more effective
645 insemination. Approaches that have been used to probe the functions of contest
646 behaviour include analysis of escalation patterns and the energetic costs of performing
647 and receiving agonistic behaviours. As Mowles and Ord (2012) have already pointed
648 out, similar approaches could be applied to reproductive behaviour, in this instance in
649 relation to metrics of skill.

650 **Question 3: What constrains skill?** If skilful reproduction contributes to success, why
651 is there variation in skill across individuals? Analyses of hermit crab shell fights (Briffa &
652 Fortescue, 2017; Lane & Briffa, 2020) and human boxing show that skill declines as
653 fights progress (El Ashker, 2011), indicating that energetic demands constrain the
654 coordinated movement patterns required for skilful fighting. Furthermore, skill covaries
655 with vigour (Briffa & Fortescue, 2017; Lane & Briffa, 2020), such that individuals that
656 fight skilfully are also capable of fighting with high vigour, potentially because efficient
657 movement allows greater vigour, possibly through reduced energetic expenditure. Skill
658 may also reflect life-history trade-offs in which investment in the neuromuscular
659 apparatus required for skill could trade-off against other traits such as longevity
660 (alternatively skill may improve with experience and thus provide information on age).
661 Thus variation in reproductive skill could reflect both short-term energetic status and
662 motivation as well as alternative life-history strategies.

663 **Question 4: Do performance traits trade-off with each other?** Following on from
664 questions 2 and 3, if skill can facilitate elevated vigour and if there are constraints on
665 skill, this points to the possibility that skill may be involved in trade-offs with other
666 fighting traits. This may include trade-offs among different components of skill but also
667 the possibility of trade-offs between components of skill and vigour, and between
668 behavioural and morphological (i.e. weapons or defenses) contest traits. For example, a
669 high rate of activity might be favored over high precision, or a large weapon might be
670 favored over efficient movement. As with other life-history traits, such trade-offs may
671 result from selection but could also be modified by developmental experiences.
672 Furthermore, trade-offs between the different components of agonistic behaviour might

673 change facultatively, such that tactics can be adjusted between and within fights. In
674 order to investigate such trade-offs directly it would be necessary to manipulate the
675 components of interest. This might involve applying physical constraints or adjusting
676 energetic status e.g. by pre-exposure to different oxygen saturations in the case of
677 aquatic animals (Briffa & Elwood, 2000b, Lane & Briffa, 2018).

678 **Question 5: Is skill a heritable personality trait?** Finally, if the effects of skill, its
679 functions and proximate constraints have been established, we should turn to the
680 question of the origins of individual differences in skill. In other words we could ask
681 whether skill is a personality trait in the sense of being repeatable across reproductive
682 encounters, to what extent it is plastic across mating partners, and to what extent
683 individuals differ in this plasticity. As discussed above, by examining precision in
684 contests and courtship we are already investigating a variance component of
685 repeatability that might show significant variation across individuals in its own right. If
686 reproductive skill is significantly repeatable, researchers could then turn to the question
687 of whether it is heritable and thus whether reproductive skill (including the capacity to
688 acquire it through experience) could arise through inter-sexual, intra-sexual or natural
689 selection.

690

691 Herein, we have argued that skill, a performance trait of known importance for contest
692 success, could also be a trait important for driving variation in reproductive success.
693 Moving forward, assuming that our (Briffa & Lane, 2017) framework for defining fighting
694 skill (efficiency, accuracy, precision and appropriateness) can be applied to reproductive

695 skill, it seems that specific measures that quantify each of these components could
696 readily be devised for reproductive behaviour in given systems. This could provide new
697 insights into inter-and intra-sexual selection, utilizing approaches that have already
698 been applied in animal personality and contest behaviour research.

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