

Evolutionary Consequences of Social Isolation

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Social isolation has profound impacts. Most animal research focuses on negative phenotypic consequences of social isolation within individual lifetimes. Less is known about how it affects genetics, selection, and evolution over longer timescales, though ample indirect evidence suggests that it might. We advocate that evolutionary consequences of social isolation be tested more directly. We suggest that the 'index of social isolation', the mismatch between actual and optimal social interaction experienced by individuals within a population, may play a key role in releasing cryptic genetic variation, adaptation rates, diversification patterns and ecosystem-level processes. Evolutionary dynamics arising from social isolation could have significant impacts in applied settings such as conservation, animal breeding, control of biological invasions and evolutionary resilience to anthropogenic change.

Keywords: conservation, indirect genetic effects, invasion biology, loneliness, social selection, sociogenomics

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2 Social Isolation: Its Features and Prevalence

3 The psychological, physical, and societal impacts of social isolation are major research interests [1,2].
4 Despite clear connections to components of fitness such as health and well-being, little is known
5 about whether or how the experience of social isolation might change evolutionary dynamics at
6 population, species or ecosystem levels. Increasingly, there are good reasons to suspect that it might,
7 so here we articulate an evolutionary research agenda and reasons for more directly studying social
8 isolation from an evolutionary perspective. A key question is whether viewing social isolation as a
9 unitary phenomenon could provide additional insight beyond what is gained from existing
10 approaches in social evolution.

11
12 Social interactions are ubiquitous if not frequent, even amongst animals not classically considered to
13 be social. Nearly every animal has the potential to experience social isolation. Many studies examining
14 its effects understandably focus on social species, such as humans [2], other primates [3], and eusocial
15 arthropods [4], and the study of social isolation has gained most traction in human research in which
16 a well-developed literature focuses on the sociological, psychological and medical significance of
17 experiencing separation from others. Despite this, the experience of social isolation is also highly
18 relevant in species that are classified as asocial [5]. Social isolation can reflect individual behaviour,
19 such as might occur when a subordinate male in a social hierarchy terminates a detrimental social
20 interaction. It can also reflect characteristics of the environment outside the immediate control of a
21 focal individual that impede or mask signal transmission ('signal masking'), such as anthropogenic
22 pollution, habitat disturbance or signal jamming [6], literal physical separation that might occur
23 during dispersal or vicariance events [7], exclusion from a social group [8], loss of social signals [9], or
24 decreased social connectivity during conservation reintroductions [10]. Its effects may also be sex-
25 specific [11]. Social isolation thus depends on the availability, detectability, and perception of social
26 stimuli in the environment. Box 1 discusses its variation across taxa and contexts, which can be
27 complicated by a number of life history and environmental factors, and defines a standardized index
28 of social isolation to facilitate evolutionary studies.

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32 Why Study Social Isolation from an Evolutionary Perspective?

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34 Social isolation is often viewed as having pathological effects, perhaps reflecting the impact of Henry
35 Harlow's classic studies [12]. Accordingly, the impact of social isolation, either for a protracted
36 duration during an individual's lifespan or for transient periods, is most often viewed as having
37 negative fitness consequences [13]. If the experience of social isolation by individuals within a
38 population is predictable from generation to generation, then evolutionary responses to this
39 condition may be expected. Hypotheses about the adaptive significance and evolutionary causes of
40 social isolation are increasingly being tested in other animals where experimental manipulations can
41 be made readily. Table 1 describes key examples. Despite such advances, investigations into the
42 impacts of perceived isolation from conspecifics have mainly been limited to evaluating its effect on
43 individuals within their lifetimes. Comparatively little is known about trans-generational, evolutionary
44 consequences of social isolation, but the field of evolutionary biology is well-equipped to address
45 this.

46

47 Multiple subfields of evolutionary biology have spent decades interrogating the evolutionary impact
48 of variation in social environments, both from theoretical and empirical angles. The significance of
49 conspecific interactions to the evolutionary dynamics of sexual organisms is nearly axiomatic; usually,
50 there can be no sexual reproduction without social interaction at some point (though counter-
51 examples do exist, for example in externally-fertilising organisms). Nevertheless, studies of social
52 evolution have almost exclusively focused on the effects of variation among social environments, for
53 example to test adaptive benefits of sociality [14], and conditions lacking social interactions in
54 laboratory-based experimental work are often treated as negative controls [e.g. 15,16]. Such
55 experimental designs have driven extensive insights into social evolution, and are commonly used in
56 behavioural, genetic and evolutionary studies of cognitive function [17], conflict and aggression [18],
57 parental care [19,20], and other topics. From these observations, it seems plausible that the
58 experience of asocial conditions should significantly change evolutionary dynamics, as well. Asocial
59 environments are frequently atypical. Our suggestion therefore is that the standard experimental
60 paradigm can be usefully inverted, enabling researchers to view social isolation as a potentially critical
61 factor in the evolutionary dynamics of sexual organisms.

62

63 A research framework examining the role of social environments in evolution that emphasizes the
64 importance of asocial experience can focus attention on the possibility that, in some cases, the
65 absence of a social environment might be the determining factor shaping evolutionary dynamics of a
66 population, species or ecosystem. In a trivial sense, permanent social isolation precludes sexual
67 reproduction. However, it is also clear that transient episodes of social isolation can impact traits with
68 prominent fitness consequences, and it is important to note that social isolation can have benefits in
69 some circumstances, for example when crowding increases stress or competition [21]. Despite
70 progress examining how social isolation impacts the expression of phenotypes within an individual's
71 lifetime, little is known about variation in social isolation and how it affects the genetics of, and
72 selection on, such traits. We further explore these mechanisms below.

73

74 Evolutionary Consequences of Social Isolation

75

76 What is meant by an evolutionary consequence of social isolation? The question here is not whether
77 selection has historically favoured or disfavoured individual genotypes that are susceptible to social
78 isolation [22,23], or genotypes that tend to impose it upon others ('ostracism', cf. [8]); various
79 scenarios have been proposed to explain how the perception of social isolation might evolve as an
80 adaptation or by-product of selection for other functions [24]. Likewise, adaptationist arguments for a
81 function of social isolation have been developed within the field of human evolutionary psychology
82 [25], but their validity can be difficult to test and the findings not easily applied to other species.
83 Instead, we suggest that phenotypic variation of a trait, for example mate choice, might be influenced
84 by social isolation. This will necessarily influence the phenotypes exposed to selection and therefore
85 potential evolution of the trait. In addition, we suggest that variation in the timing and/or extent of
86 social isolation may itself reflect genetic variation and therefore evolve via indirect genetic effects
87 [IGEs; 26]. Box 2 describes several recent case studies that have explicitly examined the genetics of
88 social isolation.

89

90 The ability to self-impose social isolation may represent an important adaptation under certain
91 circumstances and result in social selection exerted upon other group members. Researchers studying
92 the ant species *Temnothorax unifasciatus* manipulated the manner in which colony workers died:
93 either naturally, by CO₂ exposure, or by an induced infection with the pathogenic fungus *Metarhizium*

94 *anisopliae* [4]. In all cases, dying workers removed themselves from the nest and remained socially
95 isolated until death, a behaviour that dramatically eliminated social contact with other nestmates [4].
96 Their isolation not only quarantined them from nest mates, providing an adaptive benefit that might
97 be maintained through kin selection, but it also made them die faster [4]. Transient social isolation
98 appears to mitigate some of the costs associated with group living in social species, such as increased
99 risk of parasite or disease transmission [1], although this must be balanced against the benefits of
100 social immunity [27]. In humans, the existence of ostracism behaviour itself has been suggested to
101 provide a mechanism for reducing resource monopolisation by dominant individuals in strong social
102 hierarchies, suggesting that the ability to socially exclude others can generate selection for traits
103 promoting egalitarianism [28,29].

104

105 Social isolation's multifarious, time- and context-dependent costs and benefits are likely to heavily
106 influence its effects on evolutionary dynamics. However, for social isolation to exert a significant
107 influence on the evolution of a population or species, one condition must be met: experience of
108 social isolation by an individual or individuals within the population must either change the genetic
109 variation available to the action of selection, or it must change the action of selection itself. Either of
110 these can be accomplished in a number of ways, and Box 3 details several case studies. There is
111 evidence that social isolation can change gene expression [30] and induce epigenetic modifications
112 [17,31]. The experience of social isolation also clearly affects fitness traits, for example by altering:
113 mate choice and reproductive success [18,32], immunity or disease state [13,33], endocrine profiles
114 [34,35], cooperative predator detection [36], communication [37], social competence [38], and the
115 microbiome [39]. In a number of species, social isolation increases the likelihood of same-sex sexual
116 behaviour (e.g. the fruit fly *Drosophila melanogaster* [40], the guppy *Poecilia reticulata* [41], Hermann's
117 tortoises *Testudo hermanni* [42], and the zebra finch *Taeniopygia guttata* [43]). If fitness effects of
118 social isolation are distributed non-randomly with respect to genotypes in a population, this can
119 further impose an altered regime of social selection.

120

121 The manner by which social isolation might change the genetic architecture of traits can be usefully
122 investigated from two perspectives. The first is by considering social isolation as an environmental
123 factor which causes the release of cryptic genetic variation [44]. Standing genetic variation may not
124 contribute to phenotypic variation when the social environment is relatively stable across generations;
125 such cryptic genetic variation is hidden from selection. However, social isolation abruptly induces an

126 environmental change, which could cause the expression of this previously masked genetic variation.
127 Release of cryptic variation after environmental perturbation is a well-known phenomenon [45]. Even
128 if a typical social environment is restored, the imprint of phenotypic effects caused by isolation may
129 persist and provide a new phenotypic substrate upon which selection can act. Secondly, different
130 genotypes might respond differently to asocial environments; such gene-by-social environment
131 interactions can alter evolutionary potential by changing the outcome of sexual selection and exerting
132 indirect genetic effects [46,47]. Consistent with this, specific genetic mutations in a mouse model have
133 been linked to variation in sensitivity to social isolation [23]. Combined with findings from Rhesus
134 macaques that the tendency to experience social isolation is variable and repeatable in a more
135 naturalistic setting [3], and field crickets (*Teleogryllus oceanicus*) which show crossing reaction norms
136 for mate discrimination after experiencing social versus asocial rearing conditions [48], gene-by-social
137 environment interactions coupled with the release of cryptic genetic variation suggests a plausible
138 mechanism driving evolutionary consequences of social isolation, and a promising avenue for future
139 research.

140
141 With respect to how social isolation might alter selection, the most intuitive route to such an outcome
142 is through changes in social selection. When behavioural [49], neural [50], physiological [35],
143 morphological [15], immunological [27] and other traits change after experiencing social isolation,
144 how then do those phenotypic changes impart different selection on other individuals during
145 subsequent social interactions? Theoretical quantitative genetic models of social selection have
146 illustrated the link between social interactions, their genetic causes, and changes in social selection
147 [51]. Experiments which manipulate social isolation and quantify the impact on later episodes of
148 selection would be particularly useful for testing how social isolation impacts selection, and we
149 describe approaches for studying the evolutionary consequences of social isolation in Box 3.

150 Evidence that Social Isolation Impacts Evolution

151 Several recent studies shed light on the evolutionary impact of social isolation. Most evidence that
152 has accumulated for an evolutionary role of social isolation is indirect – for example, studies
153 consistent with Kaneshiro’s hypothesis suggest that the relative isolation of founding populations
154 favours the evolution of relaxed mating preferences [7], or studies that reveal substantial fitness
155 consequences of social isolation. Work characterising how the experience of asocial versus social

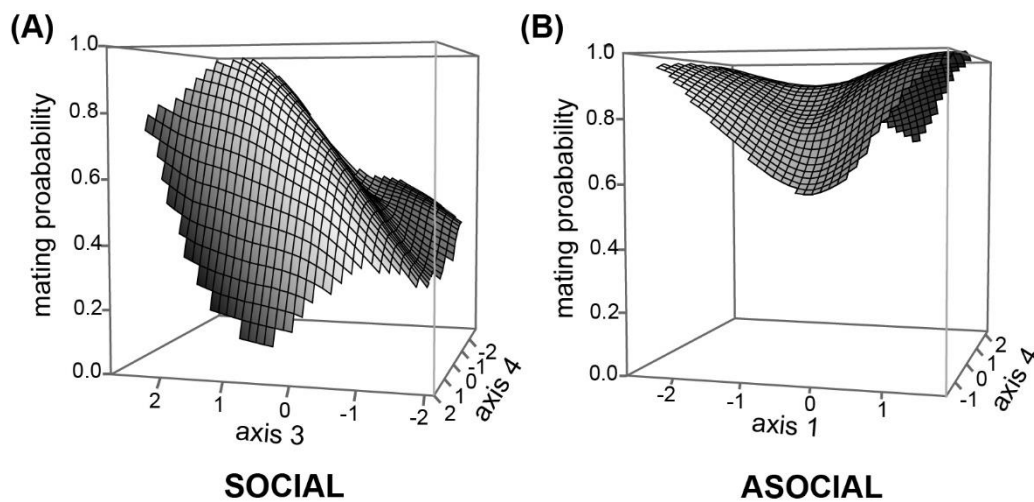
156 conditions alters the shape of selection provides further indication of how social isolation affects the
157 potential for evolutionary change.

158

159 A study of the field cricket *Gryllus pennsylvanicus* quantified how social experience changed the
160 shape of multivariate sexual selection on male traits such as age, size and condition [52] (Figure 1).

161 Females that had been socially isolated during development exerted considerably less sexual
162 selection on males compared to females that had developed in an environment with access to
163 conspecifics. In this case, female social isolation so dramatically decreased the opportunity for sexual
164 selection on males (variance in relative fitness, I [53]) that it was undetectable: from $I = 0.760$ after
165 experiencing social conditions to $I = 0.151$ after experiencing isolated conditions. This difference
166 manifested as a “flattening” of the multivariate selection surface imposed by female choice. It is
167 logical to predict that such a reduction in the opportunity for selection would translate to less rapid or
168 less pronounced evolutionary change.

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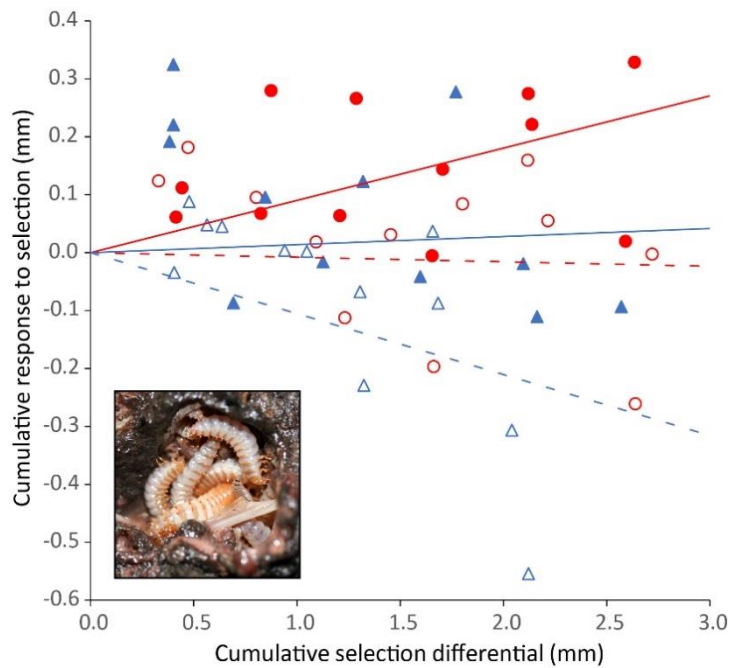
171 Figure 1. Multivariate fitness surfaces illustrating how female social isolation affects sexual selection on four male
172 traits (head width, pronotum length, residual mass and mean age) in the cricket *Gryllus pennsylvanicus* [52]. The
173 relationship between male mating probability (y-axis) and two multivariate axes on which traits were loaded
174 most heavily is shown for females that had been reared to adulthood in a mixed-sex social group (A) versus
175 females that had experienced asocial conditions from their penultimate juvenile instar onward (B). Females
176 reared in social conditions exerted strong and significant linear selection ($\theta_1 = 0.737$) on axis 3, for which male
177 size attributes loaded heavily, whereas selection imposed by inexperienced females was weaker and quadratic
178 ($\lambda_1 = 0.125$). Additionally, experienced females exerted significant net selection favouring older males
179 (standardised selection differential $s = 0.210$, $p = 0.034$), but net selection exerted by socially isolated females
180 was undetectable (all $p > 0.203$). Figure re-drawn with permission from [52].

181

182 Studies of a different insect, the burying beetle *Nicrophorus vespilloides*, have begun to document
183 such cross-generational responses to selection using laboratory populations experimentally evolved
184 with or without parental care. Burying beetle larvae develop on dead mammal carcasses and are
185 sometimes provisioned with food by their parents. The extent of this parental care varies in nature
186 and across *Nicrophorus* species [54]. An experimental evolution study reared larvae with or without
187 parents for seven generations and then split each experimental population into artificial selection
188 treatments for small versus large size [55]. The researchers measured realized heritability of adult
189 body size and responses to the artificially imposed selection regime and found that the heritability of
190 size in beetles evolving without care was low, but only when under selection for large size (Figure 2)
191 [55]. In contrast, social isolation enhanced responses to artificial selection for small size, confirming
192 that the evolutionary effects of socially isolating conditions are likely to be context-dependent [55].

193
194 Work exploring the genetics of parenting behaviour in this system has probed the role of
195 neuropeptide F (*npf*), a candidate gene with known functions in feeding. In *N. vespilloides*, expression
196 of *npf* and its receptor, *npf receptor*, vary depending on the social experience of parents; isolated
197 adults upregulate *npf* compared to adults exposed to larvae, in a way that could control the
198 appropriate expression of feeding behaviour when larvae are present [56]. Social isolation also
199 changes overall patterns of gene expression. When in the presence of their mate, males have little
200 overlap with the gene expression of the parenting female and do not participate in parenting
201 themselves [57]. If the female is absent, though, male gene expression is very similar to the female
202 and he is an equally competent parent [57].

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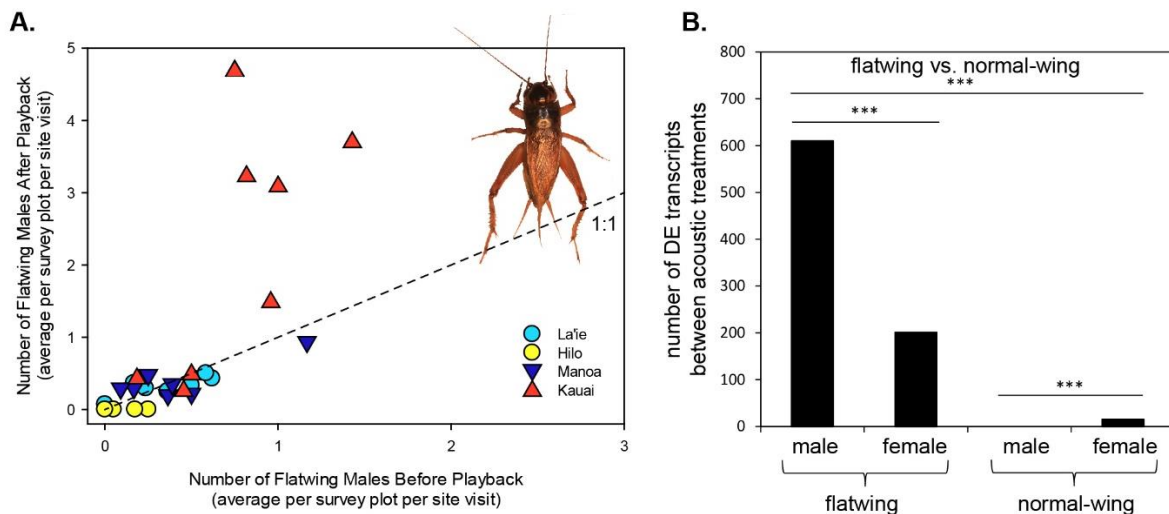
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205 Figure 2. A specific form of social isolation (from parents) changes evolution in the burying beetle *Nicrophorus*
206 *vespilloides*. An artificial evolution experiment examined realised heritability of body size in different social
207 selection regimes over seven generations [55]. Artificial selection for large larval size (red symbols) was only
208 effective when parental care was present (solid circles, solid line). Under this selective regime, persistent
209 isolation from parents (open circles, dashed line) dampened the potential for evolution of body size. The
210 opposite pattern was observed under an artificial selection regime for small larval size (blue symbols). Isolation
211 from parents potentiated evolutionary responses for small size (open triangles, dashed line) whereas parental
212 care dampened evolution of smaller size (solid triangles, solid line). Lines are regressions fitted to a zero
213 intercept; their slope is the realised heritability of body size. The inset figure shows larvae feeding on a mouse
214 carcass. (Graph redrawn with permission from [55]. Photo: Allen J. Moore).

215

216 In the burying beetle study, a lack of parental care does not equate to complete social isolation,
217 because larvae developed together on carcasses even when parents were absent. However, persistent
218 isolation from a crucial social interaction across multiple generations was shown to affect the genetics
219 and response to selection of adult larval mass, a key fitness trait. A different experimental system has
220 examined the impact of the evolutionary loss of a conspicuous sexual signal in the wild (Figure 3). In
221 Hawaiian populations of the field cricket *Teleogryllus oceanicus*, singing males risk being infested by
222 larvae of an acoustically-orienting endoparasitoid fly, *Ormia ochracea*. A male-silencing mutation
223 called *flatwing* eliminates sound producing wing structures, protecting males from attack because the
224 flies can no longer locate them [9]. Flatwing males were first detected around the turn of the last
225 century and rapidly spread on multiple Hawaiian islands, and a key feature of this system is that the
226 adaptive genetic variant causing flatwing eradicates the species' dominant long-range social signal –

227 male song. In a population on the island of Kauai in particular, over 95% of males are flatwing, a
 228 proportion that has remained stable for a decade [58], but which means that unless they happen to
 229 be in physical contact, crickets in this population effectively experience social isolation. Recent
 230 transcriptome profiling of the brains of crickets that carry genotypes for the normal, sound-producing
 231 wing type and crickets that carry genotypes for the male-silencing flatwing genotype found that
 232 crickets carrying genetic variants for flatwing are more sensitive to conditions of social isolation [30].
 233 This genetic difference in susceptibility to social isolation appears to have coevolved with the rapidly-
 234 spreading genetic variant(s) that cause flatwing, and continuous behavioural monitoring of multiple
 235 Hawaiian populations suggests that compensatory responses to social isolation experienced by
 236 individuals developing on Kauai may have potentiated rapid adaptive evolution in this system [58].
 237



238
 239 Figure 3. Behavioural and gene expression responses to social isolation in rapidly-evolving field crickets
 240 (*Teleogryllus oceanicus*). (A) A decade-long behavioural study compared the responsiveness of flatwing male
 241 crickets (pictured, inset) to acoustic playbacks in four Hawaiian populations on three islands [58]. The
 242 behavioural assay compared numbers of crickets in survey plots before and after artificially playing back island-
 243 specific calling song. The graph shows the differential in numbers of crickets before vs. after the playback, with
 244 parity indicated by the dashed line. In the population on Kauai (red triangles), which has consistently contained
 245 nearly 100% silent flatwing males and thus a high perception of social isolation due to the lack of acoustic
 246 signalling, flatwing males are on average more likely to approach artificial playbacks. A similar pattern (not
 247 shown) is seen for females. (B) Crickets of both sexes carrying the *flatwing* genotype show a constitutive
 248 difference in their sensitivity to acoustic social signals in the environment for genes expressed in the brain [30].
 249 Carriers of *flatwing* mutation(s) differentially express a greater number of genes when exposed to social
 250 isolation vs. a typical acoustic environment, consistent with the rapid coevolution of plasticity with adaptive
 251 genetic variants. (Graphs redrawn with permission from [58] and [30]. Photo: Nathan W. Bailey).

252
 253

254 Evolutionary dynamics that change as a result of social isolation might be particularly acute at the
 255 edges of range expansions, in initial founding propagules during biological invasions, or when
 256 anthropogenic activity fragments habitat. For example, the relative benefit of social feedback is
 257 enhanced at the extremes of an expanding range in the damselfly *Ischneura elegans*, promoting
 258 further range expansion [59]. Another intriguing example occurs in the invasive cane toad, *Rhinella*
 259 *marina* (Figure 4). In Australian populations at the leading edge of the toad invasion, there are few,
 260 but fast, individuals. Assortative mating has favoured long-range dispersers at the invasion front [60],
 261 but this in turn generates low-density populations and conditions of relative social isolation in newly-
 262 founded habitats [61]. A study examining the effect of these factors used toads from a recently-
 263 colonized (< 3 years) population in Western Australia to compare with toads from populations that
 264 had been evolving under relatively constant, high densities for approximately 80 years in eastern
 265 Australia and Hawaii [62]. Social attraction differed among the populations in a manner consistent
 266 with selection imposed by social isolation at the invasion front: toads of both sexes from the newly-
 267 established population in Western Australia were more likely to approach a social partner and spend
 268 more time with that individual. The authors concluded that increased social attraction at the range
 269 edge might beneficially increase information transfer and the likelihood of mating, suggesting that
 270 social isolation in such conditions might impose selection for adaptations to cope with it [62].

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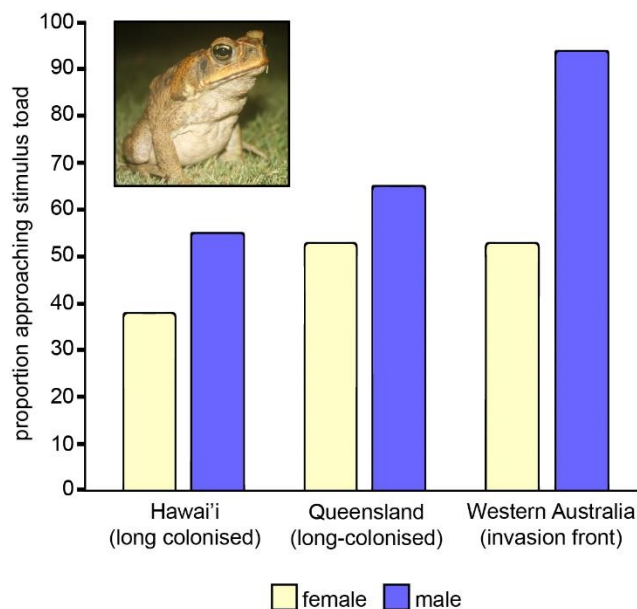


Figure 4. The effects of social isolation in invasive cane toads (*Rhinella marina*). The toads (inset photo) are exotic invaders in Hawaii and Australia. Colonies have persisted for many generations in Hawaii and Queensland, but the invasion front is comparatively new in Western Australia. Populations tend to be sparse at the invasion front, and a toads from a population at the invasion front exhibit more affiliative behaviours. Males' increased tendency to approach a fixed stimulus toad is illustrated. Such responses to social isolation, whether evolved or plastic, could have a positive impact on the success of invasive species. (Graph redrawn with permission from [62]. Photo: Nathan W. Bailey)

289 Conclusions and Recommendations

290 Animal social interactions are simultaneously traits and environments. This duality has been
291 recognized for over a century and a half, theoretically modelled as evolutionary feedback since the
292 origins of the Modern Synthesis, and still forms the basis of lively modern debate about the adequacy
293 of standard evolutionary theory. It is thus unsurprising that researchers have focused on the many
294 ways in which social environments, and individual animals' sensitivity to variation in those
295 environments, affect the evolutionary process [63]. We propose to capitalize on the theoretical and
296 conceptual frameworks that have been developed as a result of this research activity, to study the
297 ultimate causes and consequences of social isolation in animals. Useful frameworks for doing so
298 include quantitative genetic theory on indirect genetic effects and gene-by-social environment
299 interactions, in which a deficit of social interaction or asocial environments can be modeled and
300 empirically manipulated. Neurogenetic approaches allow for the control and assessment of candidate
301 genetic pathways that regulate the perception and reaction to social information in the environment.
302 Large-scale experimental evolution studies can examine evolved responses to isolation from
303 important social interactions such as parental care or sibling rivalry. And field studies of organisms for
304 which dominant social signals have been lost or masked in nature enable researchers to assess the
305 impact of social isolation in natural systems.

306
307 Why would such research activity be useful? What is the use of focusing on asocial conditions, when
308 most of what defines animal life is its social structure? The fundamental dominance of social
309 behaviour in evolutionary biology [64], and the preponderance of adaptations for, and unrelenting
310 need to navigate, social interactions provides an answer to this question: to quote Mary Jane West-
311 Eberhard, "Individuals of social species having these specialized characteristics are in a sense trapped
312 into group life, and group living may become virtually "obligatory" for them." [65, p.224]. Apart from
313 providing data that can further inform the adaptive value of social isolation in different systems,
314 understanding the mechanisms by which social isolation exerts evolutionary consequences can inform
315 the processes underlying the evolutionary origins of group life to begin with. Moreover,
316 understanding the evolutionary consequences of socially isolating animals will have relevance in
317 applied contexts where such isolation may be an outcome of human activities, such as animal
318 breeding, conservation reintroductions, efforts to control habitat loss and fragmentation in sensitive
319 ecosystems, and adaptation to a changing environment. Multiple lines of evidence suggest that social

320 isolation deserves serious evolutionary treatment. Some of its effects might be counter-intuitive, and
321 researchers should be alert to the possibility that its fitness consequences will not always be negative
322 [66,21]. We advocate grounding its study in rigorous, quantitatively-informed genetic frameworks.
323 Hypothesis testing and manipulative experiments are essential. And finally, the observations we have
324 outlined in this article hint that human society might be well-advised to reflect upon factors that
325 contribute to our own social isolation, such as changes in the quality of social interaction driven by
326 the proliferation of social media, and contemplate the long-term consequences of societal and
327 cultural shifts in the way that we perceive and cope with social isolation.

328

329 *Loneliness –*
330 *dangling from a nail,*
331 *a cricket.*

332

333 *~Matsuo Bashō (1644-1694)^[67]*

334

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515 Box 1. What is Social Isolation? Perception versus Reality

516 Is social isolation simply a physical separation from other individuals which blocks all social sensory
517 information in the environment? Social stimuli such as visual, olfactory, acoustic and tactile cues are
518 both emitted and received by individual animals. The experience of social isolation by a focal
519 organism therefore depends only partly on actual separation from conspecifics; the experience of
520 social isolation and its attendant phenotypic effects can also arise from the inability to produce or
521 receive such stimuli [35]. In addition, different modalities and types of social stimuli might not be
522 equally important [68], and the timing of periods of isolation across the life course can determine its
523 phenotypic outcome [69,38,49]. We suggest that social isolation can be measured phenotypically as
524 an individual's deviation from a population-level optimum. Assuming weak stabilizing selection and
525 evolutionary equilibrium, the optimum level of social interaction is estimated as the population mean.
526 Social isolation can then be measured as the signed deviation from the mean for each individual,
527 where negative values represent a deficit of social interaction: i.e. an individual's index of social
528 isolation. The index of social interaction is thus a quantitative measure and allows for quantitative
529 genetic treatment, examination of threshold dynamics, and standardized comparison across groups,
530 populations or taxa in evolutionary studies. The index of social isolation accounts for the fact that
531 what drives the experience of social isolation will vary widely across contexts, and might unevenly
532 impact different fitness traits [11].

533

534 In the European starling *Sturnus vulgaris* for example, visual contact with conspecifics has been
535 suggested to be a basic need for appropriate functioning, or social competence, and the requirement
536 for social visual contact may even be primary to non-social needs [70]. Researchers tested a similar
537 idea in wolf spiders (*Schizocosa ocreata*) by manipulating juvenile females' experience of male sexual
538 signals [71]. Male signals occur in different modalities: they produce percussive vibratory signals
539 transmitted through substrate, and visual signals arising from dark bristles on their legs. A lack of
540 vibratory signals experienced during development decreased adult receptivity to vibratory signals
541 during later no-choice trials; adult receptivity in the visual channel was not impaired to the same
542 extent by a lack of juvenile visual experience [71]. Despite this, females preferentially responded to
543 multimodal signals regardless of their prior experience [71]. Mate choice in swordtails also depends
544 on both visual and olfactory signals. Females' preferences develop through exposure to conspecifics,
545 but the timing of exposure and development differs for the two modalities [72].

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547 The timing and duration of social isolation can also change its phenotypic outcome. In the ant
548 *Aphaenogaster senilis*, hydrocarbons function as important social signals that control nestmate
549 recognition and are repeatedly exchanged among individuals during physical encounters. This social
550 feedback plays a key role in the maintenance of the hydrocarbon profiles of individual ants, and social
551 isolation causes the profiles to change rapidly [73]. With progressively longer durations of social
552 isolation, ants' hydrocarbon profiles changed more extensively, with corresponding increases in the
553 likelihood that they would be attacked by former nestmates upon reintroduction [73].

554

555 Using a transgenic mouse model, researchers evaluated the effect of psychosocial stress during
556 adolescence by imposing three weeks of social isolation during this critical developmental period [74].
557 In this study, group-housing acted as the control condition. The researchers found that social
558 isolation epigenetically modified the gene *tyrosine hydroxylase*, disrupting glucocorticoid signaling.
559 Through a series of experimental treatments, they isolated this adverse neurogenetic effect of social
560 isolation to the first week, and only the first week, of adolescence, identifying a key developmental
561 window during which social isolation exerts a significant phenotypic impact [74]. Despite relatively
562 brief developmental timeframes for the experience of social isolation to exert a phenotypic influence
563 on focal individuals, the effects of even transient exposure to asocial conditions can persist
564 throughout an individual's lifetime [31,69].

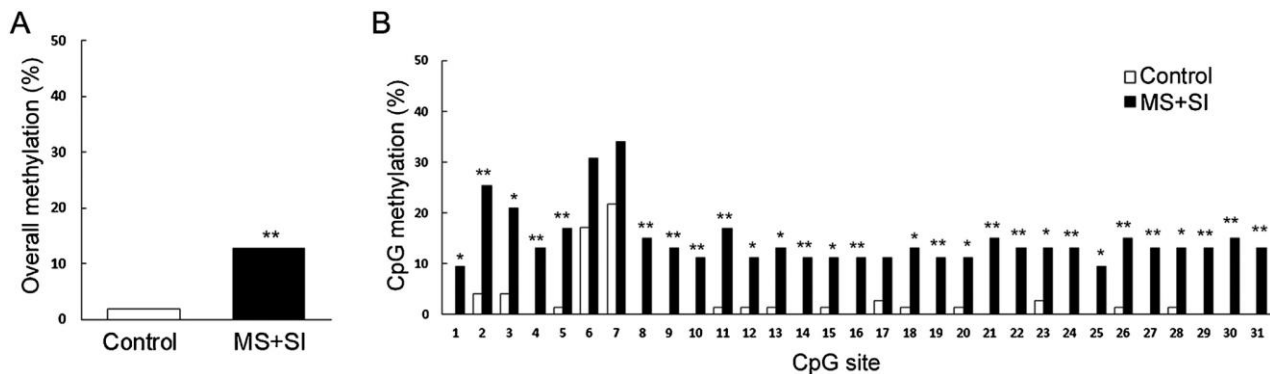
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566 Box 2. Genetics of Social Isolation

567 Recent studies have sought to characterize the genetic basis of perceived social isolation, for example
568 by partitioning genetic variance underlying familial resemblance for loneliness in humans [22]. A
569 recent genome-wide association study was unable to identify causal variants, despite evidence for
570 moderate heritability of loneliness in humans [75]. A study of Rhesus macaques (*Macaca mulatta*)
571 used a social network approach on a dataset that spanned approximately half of an adult lifespan,
572 uncovering repeatable differences in several measures of the degree to which individuals were
573 socially isolated [3]. These repeatable differences in social isolation suggest the potential for
574 underlying genetic effects, but may also arise from general social network stability.

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576 Neurogenetic studies in model organisms have addressed questions about social isolation's impacts
577 by examining candidate genes with suspected functions in social behaviours. A study of rats
578 examined the effect of social isolation on brain-derived neurotrophic factor (BDNF) expression, which
579 has been related to cognitive functioning [17]. Adolescent rats were subjected to two weeks of either
580 social isolation or group conditions with two conspecifics. Following the experimental treatment, all
581 rats were resocialized. Those that had experienced social isolation later showed impaired prepulse
582 inhibition, i.e. a decreased neural capacity to process external stimuli without interruption [17]. This
583 neural impairment was associated with acetylation modifications to the BDNF gene and
584 corresponding changes in BDNF expression in the medial prefrontal cortex and hippocampus of
585 isolated rats' brains [17]. In mice, epigenetic gene regulation also controls changes in the expression
586 of neural dopamine receptors following social isolation, suggesting functional genetic mechanisms
587 involving dopaminergic neurotransmission and the potential for long-term, trans-generational
588 phenotypic responses to social isolation [31] (Figure I).

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593 Figure I. Social isolation causes gene expression changes via epigenetic modification in mice [31]. Newborn
594 mouse pups were separated from maternal contact and from contact with other pups for three hours on a daily
595 basis for two weeks. In females, the experience of social isolation caused decreased food seeking behaviour,
596 which was consistent with a change in dopaminergic reward systems of the brain. The involvement of brain
597 dopamine circuits was supported by the observation that social isolation reduced both mRNA and protein
598 expression levels of a dopamine receptor gene (*Drd1a*) in the nucleus accumbens. This downregulation appears
599 to be caused by hypermethylation of the *Drd1a* gene in socially isolated females (MS+SI), shown in (A) above.
600 (B) Methylation status was assessed at 31 sites within *Drd1a* (CpG sites in figure above); significant differences in
601 methylation status were found in 29 of these, with all cases indicative of hypermethylation following social
602 isolation. Figure reproduced with permission from [31].

604 Box 3. Approaches for Testing the Evolutionary Role of Social Isolation

605 Clearly identified hypotheses are essential for investigating social isolation from an evolutionary
606 perspective [26,51,76] (Table 1), and several well-established frameworks could be used to test them.
607 For example, variance partitioning approaches using interacting phenotype theory can quantify the
608 impact of variation in the social environment on additive genetic variation, heritability, and
609 opportunity for selection [26]. If the genetic background of interacting partners is experimentally
610 manipulated, IGEs exerted by interacting partners that have experienced social versus asocial
611 environments can be quantified and compared, allowing a test of whether social isolation is likely to
612 potentiate or stymie evolutionary change [77]. Calculation and comparison of selection coefficients
613 using standard regression-based techniques provides an additional dimension of information [53],
614 and there is similarity to testing the evolutionary consequences of social networks [78].

615
616 Quantifying the effects of social isolation on genetics and selection is informative, but the insights
617 gained are mostly limited to how social isolation affects evolutionary *potential*, as opposed to realised
618 evolutionary change. Experimental evolution approaches provide a powerful means for manipulating
619 and observing those sorts of evolutionary changes. Experimental evolution lines of the fruit fly
620 *Drosophila pseudoobscura* provide an instructive example. Lines have been maintained for over 100
621 generations under different mating system regimes; while not reflecting any period of absolute social
622 isolation *per se*, the monogamous treatment pairs one female with one male, while females evolved
623 under polyandrous conditions have access to either 3 or 6 males [79]. Experimental removal of sexual
624 selection has been found to drive evolutionary changes in male mating investment [79], female
625 fecundity [80], male courtship song [81] and gene expression [82]. While these social manipulations
626 were performed to test the effects of mating system, they provide a blueprint for how populations
627 that contain individuals with different indices of social isolation could be experimentally evolved.
628 Many species might not be amenable to such laboratory-based experimental evolution approaches,
629 but the existence of segregating marker phenotypes, such as flatwing morphology in the cricket
630 example above, or discrete colour morphs in the damselfly *Ischnura elegans* [83], could be used to
631 measure evolutionary responses after manipulating social isolation of different morphs. Comparative
632 work examining natural populations or taxa that vary in their degree of social isolation would also
633 help to validate experimental findings against observations from natural systems, and this can be
634 coupled with sociogenomics approaches [84] to dissect the underlying genetics.

635

636 Table 1. Predicted Evolutionary Causes and Consequences of Social Isolation

637

Hypothesis	Prediction	Example	Refs
EVOLUTIONARY CAUSES			
Self-Quarantine	Social isolation prevents disease and pathogen transmission to kin	Social isolation is maintained by kin selection as a colony-level defense against pathogen transmission in the ant <i>Temnothorax unifasciatus</i> .	[4]
Ostracism	Social exclusion of free-riding individuals protects enforcers against exploitation	Game-theoretic models found that ostracism of costly free-riders can be a stable strategy which reduces the costs associated with punishing defectors.	[8]
Social Manipulation	Individuals that threaten others with social isolation gain fitness benefits	Related to the concept of ostracism above. The threat of social isolation may be an effective means of controlling other individuals, favoring genotypes that can use and follow through such threats.	[13]
EVOLUTIONARY CONSEQUENCES			
Potentiates evolution	Social isolation exposes cryptic genetic variation to the action of selection	Field crickets (<i>Teleogryllus oceanicus</i>) that lost their dominant social signal, male song, perceive an asocial environment. However, they respond flexibly to this, enabling a rapid evolutionary response.	[30]
Inhibits evolution	Experience of social isolation reduces the opportunity for selection	Previous experience of social isolation in female crickets, <i>Gryllus pennsylvanicus</i> , reduced the amount of sexual selection they later exerted on males.	[52]
Promotes evolution of cooperation	Social isolation selects for prosocial behaviours that mitigate isolation's negative fitness effects	Experimental evolution studies in <i>Nicrophorus vespilloides</i> show that consistent isolation from parental care drives higher levels of larval cooperation.	[55]
Drives evolution of greater social affinity	As above, social isolation selects for prosocial behaviours that mitigate isolation's negative fitness effects	Comparatively isolated cane toads (<i>Rhinella marina</i>) at an invasion front exhibit increased social attraction compared to those from long-established, denser populations.	[62]

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655 Glossary

656 Cryptic genetic variation: genetic variation that remains unexpressed at the level of observable
657 phenotypes, unless environmental circumstances change.

658 Gene-by-(social) environment interaction: when the genotypic contribution to trait variation differs
659 across environments.

660 Index of social isolation: mismatch between the frequency and quality of social interaction required to
661 optimise fitness, and an individual's experienced frequency and quality of social interactions.

662 Indirect genetic effects: when genes expressed in social partners alter trait expression in focal
663 individuals.

664 Loneliness: in humans, a mismatch between required levels of social interaction and perceived levels
665 available in the social environment [13] (contrast with 'index of social isolation').

666 Ostracism: exclusion of individuals through the coordinated action of a larger group [8].

667 Signal masking: when the detection threshold for a signal is increased because of the presence of
668 other signals (noise) in the environment

669 Social competence: the intrinsic ability of an individual to optimize their social behaviour to their
670 social environment [85].

671 Social immunity: group-level defenses against infection which benefit individuals.

672 Social selection: selection arising when individual fitness is affected by social competition with
673 conspecifics [65].

674 Sociogenomics: an integrated approach using techniques such as genome-sequencing, gene
675 expression profiling, proteomics, and behavioural assays to understand the genetic and
676 environmental pathways that influence social traits [84].

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