How to behave when marooned:

The behavioural component of the island syndrome remains underexplored

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Abstract: — Animals on islands typically depart from their mainland relatives in assorted aspects of their biology. Because they seem to occur in concert, and to some extent evolve convergently in disparate taxa, these changes are referred to as the “island syndrome”. While morphological, physiological, and life history components of the island syndrome have received considerable attention, much less is known about how insularity affects behaviour. In this paper, we argue why changes in personality traits and cognitive abilities can be expected to form part of the island syndrome. We consider the ecological drivers that may induce such changes, and the mechanisms through which they might occur. Finally, we provide an overview of studies that have compared personality traits and cognitive abilities between island and mainland populations, or among islands. Overall, the pickings are remarkably slim. There is evidence that animals on islands tend to be bolder than on the mainland, but effects on other personality traits go either way. The evidence for effects of insularity on cognitive abilities or style is highly circumstantial and very mixed. We conclude that our knowledge of the behavioural and cognitive responses to island environments remains limited, and we encourage behavioural biologists to make more use of these “natural laboratories for evolution”.

Keywords: — animal behaviour, behavioural syndrome, cognition, island evolution, personality.
1. Introduction

Animals and plants inhabiting islands tend to deviate from their mainland relatives in multiple aspects of their morphology, physiology, behaviour, and life history; a pattern referred to as the “island syndrome” [1-3]. A large body of literature on a variety of animal taxa documents how island populations stand out in body size and shape, colouration, locomotor abilities, diet, niche width, fecundity, and life span, for instance (reviews in [2-7]). Curiously, far fewer studies have examined behavioural modifications in island dwellers. Apart from the well-documented phenomenon of “island tameness” (insular prey species often fail to recognize or respond adequately to predators; [8,9]), whether and how insularity affects the behaviour of animals has received far less attention. This is unfortunate, because behaviour is such an important part of the phenotype, and because many of the drivers of morphological, physiological, and life history evolution on islands are also likely to impinge on behavioural characteristics. In this paper, we review the empirical evidence for a behavioural component of the island syndrome, focusing on two interrelated [9] behavioural domains: animal personality and cognition. We also consider the mechanisms and ecological drivers that could produce such changes.

2. The island environment

Islands typically accommodate fewer species than mainland habitats of the same surface area [5,10]. The dearth of competitors, and especially of large predators, instigates an atmosphere of “ecological release” [12-14] that allows many insular prey species to reach much higher densities than on the mainland [15-17]. On the other hand, for many animals, dietary resources are often considered to be poor or more variable on islands compared to the mainland [18-21]. These environmental changes (i.e. poor or variable dietary resources, reduced predation pressure and interspecific competition, increased intraspecific competition) are deemed responsible for many elements of the island syndrome described, although the mechanisms through which they exert their effects on animal phenotypes often remain unstudied. We expect that the particularities of insular environments will likewise prompt modifications in the behaviour of island dwellers.

Animal personality research has revealed repeatable and heritable interindividual variation [22] in the way that animals behave in response to various external stimuli. Individual animals thus belong to one of several possible and co-existing “behavioural types” — groups that will respond in a distinctive, predictable way to challenges, even under different contexts. More specifically, individuals differ consistently in “personality traits” such as boldness, aggression, activity, exploration, and sociability (reviewed in [23]). Often these personality traits intercorrelate, giving rise to a “behavioural
syndrome” [24]. Because island and mainland habitats differ in the opportunities and challenges they offer to their inhabitants, we can expect changes in the relative frequency of behavioural types or in the way that personality traits interconnect.

Cognition is the collective of neural processes responsible for the acquisition, retention, and use of information [25] and, as such, a key determinant of fitness in vertebrate animals (e.g. [26-29]). Individuals differ in their cognitive abilities, but also in cognitive styles (e.g. learning speed versus accuracy [24]). Relatively little is known on the repeatability of cognitive testing in time, or across context [30]; or on how different cognitive scores interrelate [31]. In humans, scores on different cognitive tests tend to correlate positively, lending credibility to the concept of “general intelligence” (the so-called “g-factor”, another syndrome [32,33]). Similar covariation has been described for a handful of other mammals (e.g. [34]) and birds (e.g. [35]), but overall the evidence for a g-factor remains scarce [31,36]. Again, given how islands deviate from mainland habitats, different levels or types of cognitive skills may be favoured in both types of environments.

3. The current evidence for a behavioural component to the island syndrome

Table 1 reviews the evidence that animals from islands differ from their mainland counterparts in aspects of their personality and cognition.

Boldness. Perhaps inspired by early (mostly anecdotal) accounts of island tameness (e.g. [8,37,38]), most studies investigating the effect of insularity on animal personality have focused on boldness. Boldness, i.e. risk taking behaviour in the presence of a predator threat, is expected to change in a way that matches predation risk on islands. The vast majority of these studies confirmed that island animals, especially those living on remote, predator-poor islands, tend to be less vigilant than their relatives inhabiting the mainland or less remote, predator-ridden islands [9,39]. Reindeer (*Rangifer tarandus*) on Norwegian Edgeøya [40], bull-headed shrikes (*Lanius bucephalus*) on Japanese Nansei islands [41] and whiptail lizards (*Aspidoscelis hyperythra*) on islands in the Gulf of California [42] are exceptions, but their relative shyness is attributed to unusually high densities of predators (polar bears, rats, and human collectors, respectively) in their habitat. It should be noted that most of these studies rely on field observations of the flight initiation distance (FID), a proxy of boldness that is not without difficulties. FID is known to depend on a variety of factors related to the internal status of the animal (e.g. satiation [43]; reproductive status [44]; body condition [45]), and its environment (e.g. temperature [46]; substrate type [47]; levels of human exposure [48]; social context [49]; distance to safety [50]) — all of which may differ consistently between island and mainland sites. In addition, FID
measures boldness as an animal’s response in a single context (a human approaching), without testing whether inter-individual variation is consistent and repeatable across time and context (i.e. personality *sensu stricto* [23]). Therefore, future studies should test the boldness of island and mainland conspecifics in multiple, controlled contexts.

Increased boldness on islands is typically attributed to reduced predation pressure, although quantitative or even qualitative estimates thereof are seldom presented. The (often implicit) rationale is that bold behaviour is less penalized in predator-poor environments, and might even be favoured for its paybacks in a non-predatory context [51,52]. It should be noted that while many (oceanic) islands are indeed devoid of mammalian predators, others hold thriving populations of other predators (e.g. [53,54]). Bold anti-predatory behaviour could also evolve as a behavioural mechanism to deter some of these predators (see [55] for a curious example in New Zealand parrots). Future research on this topic should be careful to match-up behavioural traits of island animals and the predators they were exposed to through evolutionary time.

The mechanisms through which the differences in boldness arise remain unclear. Most authors consider both phenotypic plasticity (learning) and genetic adaptation, usually with a slight preference for the former. In a rare study tackling the question directly, Stratton et al. (2021) found that differences in boldness between Gough Island and mainland US mice (*Mus musculus*) persisted in the F1-generation, offering support for genetic change [56].

Explorativeness. Only a handful of studies have investigated the effect of insularity on animal explorativeness, with mixed results. Common frogs (*Rana temporaria*) on Bothnian islands [57], and giant house mice (*M. musculus*) on Gough Island [56] are more explorative than their conspecifics on the mainland; brown anoles (*Anolis sagrei*) were more inquisitive on predator-free islets rather than islets with predators [58]; and among parrots (Psittacidae) [59] and scrub jays (*Aphelocoma coerulescens*) [60], island species/populations tend to be more neophilic and explorative. Most studies indicate that predation relaxation and unpredictable resource availability may be drivers of increased explorativeness on islands [61]. Lapiedra et al. (2018) provided evidence that the behavioural changes in brown anoles (*A. sagrei*) following the introduction of a predator were due to natural selection [58]. Brodin et al. (2013) argued how dispersal-related environmental filtering could be responsible for the higher explorativeness in island common frogs and tadpoles [57]. In contrast, deer mice (*Peromyscus maniculatus*) on islands in the Canadian Winnipeg River tended to be less explorative than mainland conspecifics, possibly reflecting differences between inland and oceanic island systems [62]. Work by Camperio Ciani and colleagues showed that human inhabitants of the Egadi islands are less open to new experiences than their compatriots in mainland Italy, an observation they attribute to
disproportionally high emigration of individuals with neophilic personalities [63,64]. They even identified a genetic polymorphism that could be associated with this “personality gene flow” phenomenon [65].

Aggression. Changes in aggression could go either way. On islands, resources may be more limited and thus worth fighting for more. On the other hand, models predict that animals should stop defending territories if high population densities and the resulting excess of floaters render the monopolization of resources ineffective [66]. The empirical evidence also goes both ways. The anticipation of reduced antagonism in island populations is corroborated by studies on a few rodent species (P. maniculatus [67,68], Myodes gapperi [62], M. musculus [69]) and birds [70]. Interestingly, Baier and Hoekstra (2019) found that the difference faded in the F1-generation, indicating an important role for phenotypic plasticity [67]. In reptiles, the results are less congruent. In tiger snakes (Notechis scutatus [71,72] and common garter snakes (Thamnophis sirtalis) [73], adults (but not juveniles) fit the pattern of reduced aggression on islands, suggesting that insular conditions induce a plastic response of soothing in these animals as well. However, Pacific rattlesnakes (Crotalus oreganus) from Santa Catalina Island behave more aggressively than mainland conspecifics; perhaps because of the high number of (recently introduced) terrestrial predators on the island [74]. Skyros wall lizards (Podarcis geigeae) on smaller islets will attack conspecifics frequently, probably because food shortage forces them into cannibalism [75].

Sociability. The effects of insularity on sociability (i.e. attraction to conspecifics) have hardly been studied. Predation risk, population density and food availability are among the ecological factors suspected to influence sociality. Older papers report that meadow voles (Microtus breweri) [76] and chuckwallas (Sauromalus spp.) [77] living on islands tend to be more sociable, than closely related species on the mainland. In contrast, yellow-faced grass quits (Tiaris olivacea) [78] and birds in general [79] are seen in flocks more often on the mainland than islands. Long-tailed macaque (Macaca fascicularis) group size tends to be larger on the mainland [80]. Work on humans suggests that islanders have lower levels of extraversion and openness, and exhibit greater animosity towards strangers, keeping for instance greater interpersonal distance [63,64,81].

Activity. We found very little information on differences in the level of activity displayed by island and mainland animals. Clouded anole lizards (Anolis nebulosus) are more active on islands [82], while insular oriental fire-bellied toads (Bombina orientalis) exhibit lower activity levels compared to mainland conspecifics [83]. Predation pressure, resource availability, and thermal conditions are
considered to shape activity. The dearth of information precludes any form of generalization. This is a pity, because there is currently great interest in the causes and consequences of variation in the amount of activity that animals display (see [84]), and mainland-island comparisons might have provided a nice insight in the matter.

Overall, few studies have thoroughly investigated the effect of insularity on personality. Careful analyses of animal temperament should consider whether individual behavioural scores that are believed to reflect aspects of personality are repeatable over time and over different contexts and whether and how these aspects co-vary to produce behavioural syndromes. Inquiries into the evolution of insular personality will also require information on the heritability of such scores. Few of the studies in table 1 fulfil these conditions.

Cognition. Studies on a variety of mammals and birds report a reduction in brain size. However, interpretation and generalization of these results is problematic. First, most of these studies have been performed on fossil species, and are therefore fraught with practical difficulties concerning the estimation of brain size and body size (see e.g. the disparate results for the Siculo-Maltese dwarf elephant (Palaeoloxodon) [85,86]). Second, no evidence for insular brain size reduction was found for other species, such as the Cretan deer (Candiacervus spp.) [87], the Sardinian dhole (Cynotherium sardous) [88], or even the long-thought-dim dodo (Raphus cucullatus) [89]. Third, recent comparative studies on extant mammals [90] and crows and ravens [91], found no effect of insularity on relative brain size. A meta-analysis of over 1900 species of birds even suggests a tendency towards larger brains in insular species. The authors argue that island species require larger brains to cope with the difficulties of having to exploit novel dietary resources and deal with high environmental stochasticity [92]. Fourth, and most importantly, it has become increasingly clear that brain size must be considered a shaky proxy cognitive capacity (e.g. [93,94]). More direct evidence comes from a few studies that have compared aspects of cognitive capacity between island and mainland populations. Deer mice (P. maniculatus) from Morseby Island solved a water-maze task faster than conspecifics from mainland British Columbia, but this was attributed to differences in swimming rather than cognitive skills [95]. White-faced capuchins (Cebus capucinus) from a single island in Coiba National Park, Panama, engage in innovative tool use, a behaviour never observed in mainland conspecifics [96]. Tool-use is also remarkably often reported in island birds (e.g. New Caledonian crows (Corvus moneduloides) [97], Hawaiian crows (Corvus hawaiiensis) [98], woodpecker finches (Cactospiza pallida) [99], Goffin’s cockatoos (Cacatua goffini) [100]), but no one seems to have checked for a general association...
between tool use and insularity. On the whole, the number of studies examining the evolutionary fate of cognition, intelligence, and behavioural flexibility on islands is very limited.

4. Routes towards insular behaviour

The studies cited in the previous section present evidence that insularisation may indeed induce considerable change in animal behaviour. Below we review the multiple mechanisms that could produce such changes (also see Fig. 1). Because these routes are rarely documented in island-mainland comparisons, some of our examples come from other study systems. However, we try to explain why we think particular drivers and pathways seem likely to be especially relevant in an insular context.

4.1. Phenotypic changes

As most complex physiological and morphological traits, behavioural traits are expressed along a reaction norm, the adult outcome depending on the environmental conditions experienced during (sometimes remarkably short) time windows during their development [101-103] For instance, smaller fathead minnows (*Pimephales promelas*) behave more boldly than larger conspecifics when raised in low-risk environments, but not when raised under high-perceived risk [104]. Jumping spiders (*Marpissa muscosa*) raised in socially enriched environments (i.e. raised in conspecific groups) demonstrated higher exploration later in life [105]. Hence, key components of insular environments such as reduced predation risk and increased population density could instigate changes in personality, even without genetic differentiation.

Cognitive capacity is notoriously plastic. In humans and traditional animal models, such as rats, pigs, and guinea pigs, both intrauterine [106] and postnatal [107] undernutrition impedes neuronal and cognitive development. Effects have been observed in brain architecture, and on cognitive capacities such as spatial and reversal learning, memory and novelty seeking [106,107]. On the flip side, favourable developmental conditions are known to induce a “silver spoon” effect, with positive effects on cognitive capacity. For instance, blue tits raised on taurine-enriched diets demonstrated improved memory and learning skills [108]. Islands tend to be relatively poor in dietary resources [18-21], and this may directly and negatively impact cognitive capacity. However, due to ecological release and niche enlargement, islands may sometimes provide more food per unit effort (e.g. [109]) and thus might constitute “silver spoon” environments that boost cognitive development. Changes in foraging behaviour that accompany niche expansion may reverberate in personality [110] and cognitive [111] traits. Island dwellers may also experience different social contexts during ontogeny than their mainland relatives, as a consequence of high population density. In group-living animals, such as
Australian magpies (*Cracticus tibicen*), growing up in a rich social environment boosts performance in a variety of cognitive tasks [29,112].

### 4.2. Genetic changes

Alternatively, since both personality and cognition traits display heritable variation [24,113] any evolutionary mechanism influencing allele frequencies may cause differences between island and mainland populations.

Genetic differences may arise by chance: through a founder effect (if allele frequencies of the colonizing propagule happen to differ from that of the mainland source population), or when random drift haphazardly alters the genetic constitution of the newly established island population [114]. Raffard et al. (2018) found that the differentiation in boldness among 13 populations of a freshwater fish (the European minnow, *Phoxinus phoxinus*) could be attributed to random drift [115]. Other studies mention genetic drift as a potential cause of among-population variation in personality or cognitive traits, although often as a less glorious alternative to natural selection (e.g. [116]).

In the early stages after colonization, populations on oceanic islands may be prone to inbreeding [117], which typically results in increased homozygosity and decreased body condition [118,119]. If personality is condition-dependent (which seems plausible, but remains debated [120]), inbreeding may result in non-adaptive changes in average personality traits. In accordance, Verweij et al. (2012) found negative associations between level of inbreeding and personality traits such as novelty seeking and persistence in Finnish and Australian citizens [121]. In a rare study of the effects of inbreeding on animal personality, Müller and Juškauskas (2018) found that inbred individuals of the leaf beetles (*Phaedon cochleariae*) behaved more boldly than outbred conspecifics [122]. Evidence that human cognitive abilities may suffer from inbreeding depression comes from genealogical studies on consanguineous marriages (e.g. [123]), including those of royal lineages (e.g. [124]). These traditional studies have recently been substantiated by genome-wide association studies describing negative associations between levels of inbreeding (homozygosity) and human intelligence [125-128], demonstrating that effects on cognition are not restricted to recent inbreeding events. Studies on the effect of inbreeding on animal cognitive capacity are extremely rare [129], but inbred lines of rats tend to exhibit cognitive deficits compared to outbred lines (e.g. [130]). In fruit flies (*Drosophila melanogaster*), Nepoux et al. (2010) found a negative effect of severe inbreeding on aversive learning [129].

Differences in personality or cognitive traits between island and mainland populations could also arise through pleiotropic effects, i.e. when alleles that are selected because of their effect on unrelated morphological, physiological or life history traits also happen to shape behaviour [131-134].
More concrete evidence for such piggyback riding of behavioural genes comes from artificial selection studies, in which selection for one trait has (often unexpected) effects on other characteristics. For instance, selection for high voluntary wheel-running activity in mice resulted in reduced aggressiveness towards conspecifics [135]. Selection for wheat digestibility in broiler chickens affected the birds’ neophobia, sociability, and explorativeness [136]. In *Drosophila*, selection for both nutritional stress resistance [137] and longevity [138] came at the cost of reduced learning ability. These studies have not worked with island populations, but high locomotory activity, increased digestive abilities, nutritional stress and longer life spans have all been associated with insular conditions (e.g. [82,139,140]). As an example of how pleiotropic effects might come about at the molecular level, consider how the vertebrate melanocortin system affects a variety of traits, including coloration, immunity, energy expenditure, and stress resistance, but also aggression and sexual activity [131]. In principle, thermal conditions or camouflage requirements on islands could select for darker colouration by increasing the activity of melanocortin receptors, which would collaterally increase aggressiveness and sexual activity. Pleiotropic effects have been invoked to explain the multifaceted changes in island lizards [141], although in this study the behavioural components (aggressiveness, voraciousness) were deemed the targets of selection, and the changes in colour a happy by-product.

Perhaps the most intuitive path towards genetic differentiation in personality or cognition between island and mainland populations is through natural selection. As recognized by students of dispersal reduction ([142-144], but see [145,146]), island dwellers are likely to have been exposed to at least two successive bouts of selection during their evolutionary history: on their route to the island, and subsequently, when confronted with the new environment. The nature and even the direction of selection during these two stages may diverge strongly [147]. Trait values that facilitate dispersal to and colonization of islands may diverge from (or even oppose) those that benefit fitness once the population is established [148]. Which of the two selection bouts will be most reflected in the island population, will then depend on the time since colonization, and the plastic and/or evolutionary malleability of the trait concerned. Recent studies have documented instances of very rapid dispersal reduction in some insect and plant taxa (e.g. [145,149]), but there are also cases where dispersal capacity does not or only very slowly decreased post-colonization [150,151].

Dispersal barriers may act as a filter for or isolate island dwellers of certain personality and cognitive phenotypes. There is now ample evidence for personality-dependent dispersal (reviewed in [152,153]). Aggressiveness may influence dispersal either way. Antagonistic individuals may coerce...
more peaceful conspecifics to disperse [154,155], or move away themselves [156,157]. The relationship between sociality and dispersal tendency seems also taxon-specific (compare [158] with [159]) or density-dependent [160]. The relationship between dispersion and cognition has received little attention [161,162]. In theory, both positive and negative relationships could evolve: well-developed cognitive skills may help dispersers survive the perilous route towards new horizons; but individuals that invest heavily in cognition may be reluctant to disperse into unknown territories (e.g. [163]). Comparative research on wide a variety of animals suggests that cognitive abilities are a determinant of invasion success (reviewed in [164]), but these studies typically emphasize the role of cognition in coping with new challenges encountered in the invaded territories, rather than with the dispersal event itself.

Once arrived on an island, animals are likely to face selective pressures that diverge from those experienced on the mainland in multiple aspects (see above §2), prompting adaptive, genetic changes in their personality and cognitive traits. Although studies on how personality traits evolve in response to environmental changes remain relatively rare [23], there is now evidence that changes in ecological factors such as food availability (e.g. [165]), predation pressure (e.g. [166]), parasite load (e.g. [167]) and habitat structure (e.g. [168]), all known to occur on islands, may drive personality evolution. In addition, personality traits seem a likely target of sexual selection (see [169,170] for an overview of ideas), whose strength and direction may vary among islands (e.g. [171,172]). Proof for the evolvability of personality comes from studies of the fitness gradient in wild populations, from artificial selection studies, and from analyses comparing populations or species (reviewed in [23,173]).

Probably because it is deemed key to the evolution of our own species, theories on why and when natural selection promotes high cognitive abilities abound (see e.g. [111] for a review). They can be pushed into two major schools. The “Social Intelligence Hypothesis” (SIH) postulates that cognition has evolved to meet the challenges of a complex social life; to be able to read the intentions of peers and manipulate their behaviour [174,175]. The “Ecological Intelligence Hypothesis” (EIH) states that other, non-social aspects of the environment have steered cognitive evolution: challenges associated with locating or manipulating food, finding shelter or avoiding predation, for instance [176]. Refining EIH, the widely cited “Cognitive Buffer Hypothesis” (CBH) [177] emphasizes the role of environmental variability and argues that cognition evolved as a means to buffer individuals against stochastic fluctuations in, for instance, food availability [61,178]. Instead, the “Expensive Tissue Hypothesis” (ETH) [179] argues how low or variable resource availability could select for reduced investment in costly brain tissue (and more performant gut tissue), which might come at the expense of cognitive ability. Artificial selection studies, selection gradient studies, and comparative analyses have confirmed that cognition is indeed malleable through natural selection (see [111,180] for reviews).
Interestingly, recent comparative genomic techniques found evidence for positive selection on genes associated with brain development in multiple lineages (e.g. dolphins: [181]; paper wasps: [182]; capuchin monkeys: [183], including our own [127,184]).

In short, insularisation can affect personality and cognition for multiple reasons and through several pathways.

6. Challenges, opportunities, and avenues for behavioural research on islands

If changes in personality and cognitive skills following insularisation seem likely and important, then why have they not been studied more often? Clearly, behavioural traits tend to be highly plastic, do not fossilize well, and are difficult to compare among species, all of which complicates evolutionary studies. However, these problems are not specific to island populations, and the recent spurt in animal cognition and personality research proves that they can be overcome. Actually, we believe that island-mainland or among-island comparisons constitute a very promising avenue for studying the micro-evolution of behaviour, just as they did for other traits and for the same reason: because they offer the opportunity to study recurrent phenotypic changes in relatively simple environments [5].

A possible explanation for the dearth of work on cognition and personality performed on insular systems could be a mismatch in study organisms. Studies of animal personality and cognition have traditionally used primates, other mammals, birds and fish as models [185,186] — species that are often not very abundant on islands — especially not on smaller, oceanic islands. Recently, however, techniques for measuring personality and cognitive capacity have been tailored to and successfully applied in other taxa, such as reptiles [187] and insects [188], that can be sampled in large numbers on even the smallest islands. With the right study organisms, it should be logistically possible to study how insularity affects personality and cognition.

Clearly, a number of quality criteria must be met. By definition, personality scores should be repeatable in time and across contexts, but this has rarely been assessed in island populations. Along the same line, cognitive scores should be carefully tested for repeatability within individuals, and consistency among individuals and across contexts. Obtaining robust behavioural measurements, preferably in a number of populations and species, is a necessary first step to establish whether there is, effectively, a behavioural component to the island syndrome.

Equipped with robust data on personality traits and cognitive abilities, hypotheses on how insularity incites changes in personality or cognition can then be put to the test (Table 2). Several ideas on this matter can be formulated, but remain largely untested. For instance, inbreeding depression, through its effect on body condition [119], is thought to force individuals to adopt low-fitness, under certain ecological contexts, personalities [120]. Predation intensity is considered a prime factor...
determining the relative fitness of different personalities (e.g. [166,189]), and an important driver of cognitive evolution (e.g. [190, 191]). High population density is likely to decrease aggressiveness and increase sociality in island dwellers (e.g. [192]), and in combination with low resource availability, may constrain brain development and thus cognitive abilities [179]. In contrast, the unpredictable nature of island environments has been hypothesized to select for behavioural flexibility and, hence, superior cognitive abilities [92]. Inbreeding, predation relaxation, density compensation, and environmental stochasticity are all examples of phenomena associated with, but not limited to, island environments. Therefore, studies on the behaviour of island dwellers will be of great value to our understanding of the evolution of personality and cognition, in general.

A logical next step would be to assess whether and how personality traits and cognitive traits co-vary among themselves, and with the morphological, physiological, and life history traits traditionally implicated in the “island syndrome”. This would allow testing outstanding hypotheses on how personality differences are maintained over time [193], on the existence and consistency of cognitive syndromes and styles [194,195], on the role of behaviour in the pace-of-life theory [196], and on behavioural consequences of correlational selection on physiological or morphological traits (e.g. [197-199]).

The above questions primarily relate to the eventual outcome of evolutionary trajectories, but islands also offer unique opportunities to learn about the nature of the trajectories themselves. By studying populations of varying age (colonization history), one could assess the importance of adaptive landscapes [200], genetic covariance matrices [201] and the prevalence of “evolutionary paths of least resistance” [202] in the evolution of behaviour. Such analyses could also reveal reversals in the direction of evolution, e.g. when distinct phenotypes facilitate dispersal and settlement (cfr. [203]). Finally, studying islands with different colonization histories could reveal information on the rate at which behavioural changes occur. Such knowledge is of fundamental biological interest, but in addition may be valuable in the context of the conservation of island and other isolated populations.


27. Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., & Pravosudov, V. V. 2019 Smart is the new sexy: female mountain chickadees increase reproductive investment when


75. Cooper WE Jr, Dimopoulos I, Pafilis P. 2014 Sex, age, and population density affect aggressive behaviors in island lizards promoting cannibalism. Ethology 121, 260-269. (doi: 10.1111/eth.12335)


Figure 1: — Putative relationships between island conditions, personality, and cognition. Arrows with (1) represent ‘traditional’ pathways leading to the island syndrome. Pathway (2) echoes the Expensive Tissue Hypothesis [179], predicting lower cognitive capacity in island populations. In contrast, (3) depicts the possibility that the unpredictable nature of the island environment selects for behavioural flexibility, requiring high cognitive capacity [61]. Route (4) represents a possible connection between niche expansion, dietary specialisation, and aspects of personality and cognition (as proposed by [110,111]). Arrows with (5) indicate that high densities could lead to reduced territoriality and changes in how animals interact behaviourally (e.g. [69]). Arrow (6) summarizes the multiple connections between ‘traditional’ elements of the island syndrome and personality, e.g. through pleiotropic effects [131] or correlated selection (e.g. pace of life syndrome [196]). Pathway (7) concerns non-adaptive consequences of inbreeding on personality and cognition (e.g. [120]). Route (8) describes a possible role for selection on dispersal-related personality traits (e.g. [152]). Finally, the arrows labelled (9) summarize ideas on how personality and cognition might interact (e.g. [204]).
Table 1: — Studies that have compared behavioural, personality or cognitive (including brain morphology studies) traits between island and mainland, or among island populations/species. The ‘driver’ and ‘mechanism’ are those suggested (but not necessarily demonstrated) by the authors. FID stands for Flight Initiation Distance. The ‘type of analysis’ also indicates whether the study includes repeated within-individual measurements (personality variation).

<table>
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<th>Study species</th>
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<td>Eastern chipmunks (Tamias striatus)</td>
<td>Island chipmunks are less vigilant, but both island and mainland specimens adjust vigilance to microhabitat structure</td>
<td>Beaver Island, Michigan, USA</td>
<td>two sites on mainland Michigan</td>
<td>lower predation pressure on island (checked with camera traps)</td>
<td>unknown</td>
<td>field experiments; personality variation measured</td>
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<td>14 species of macropodid marsupials</td>
<td>animals on islands are less wary and allocate more time to foraging; no effect on FID</td>
<td>Satellite islands of Australia</td>
<td>Australia</td>
<td>predation pressure</td>
<td>acknowledges possibilities of plasticity and selection</td>
<td>field observations; comparative analysis</td>
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<tr>
<td>Reindeer (<em>Rangifer tarandus</em>)</td>
<td>island reindeer are more vigilant on the island, but response distances are the same</td>
<td>Edgeoya, Norway</td>
<td>4 sites on Spitsbergen, Norway</td>
<td>possibly higher predation (by polar bears) on island</td>
<td>response distance believed to be 'hard-wired'</td>
<td>field observations</td>
<td>[40]</td>
</tr>
<tr>
<td>Bull-headed shrike (<em>Lanius bucephalus</em>)</td>
<td>Longer FID in island shrikes</td>
<td>Kikaijima, Minami-daitojima and Nakanoshima Islands, Japan</td>
<td>3 sites on main Japanese Islands</td>
<td>risk of predation (by rats) higher on islands</td>
<td>genetic change, plasticity and dispersal-related selection are considered</td>
<td>field observations</td>
<td>[41]</td>
</tr>
<tr>
<td>11 species of Falkland island birds</td>
<td>FID is lower on island than on mainland</td>
<td>Falkland Islands</td>
<td>mainland Argentina</td>
<td>absence of terrestrial predators</td>
<td>probably innate, evolutionarily acquired, but habituation also deemed possible assumed</td>
<td>field observations; comparative analysis</td>
<td>[207]</td>
</tr>
<tr>
<td>California quail (<em>Callipepla californica</em>)</td>
<td>FID is similar on mainland and island, but SD* is smaller on islands</td>
<td>Santa Catalina Island, USA</td>
<td>California, USA</td>
<td>some predators lacking on island</td>
<td>genetic ('antipredator genes')</td>
<td>field observations</td>
<td>[208]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
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<tr>
<td>Orange-throated whiptail (<em>Aspidoscelis</em> hyperythra)</td>
<td>island lizards are more difficult to catch than mainland lizards</td>
<td>7 Gulf of California islands</td>
<td>Baja California</td>
<td>predation pressure, human collection for pet trade</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>reasoned to be genetically based, implying rapid evolution of antipredator behaviour</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>field observations</td>
<td>[42]</td>
<td></td>
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</tr>
<tr>
<td>Galápagos marine iguanas (<em>Amblyrhynchus cristatus</em>)</td>
<td>lizards on predator-free islet have shorter FIDs; although FID increases with experience, it remains insufficient to avoid predation</td>
<td>Caamaño Islet, Galápagos, Ecuador</td>
<td>St Cruz and San Cristobal Island, Galápagos, Ecuador</td>
<td>predation pressure</td>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td>release from predation narrowed the reaction norm for FID</td>
<td>field observations</td>
<td>[209]</td>
<td></td>
</tr>
<tr>
<td>Spiny-tailed iguanas (<em>Ctenosaura hemilopha</em>)</td>
<td>island lizards behave less wary and have shorter FIDs than mainland lizards</td>
<td>Cerralvo Island, Gulf of California</td>
<td>Mexico</td>
<td>low predation pressure on the island</td>
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<td></td>
<td></td>
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<td></td>
<td>no hints</td>
<td>field observations</td>
<td>[210]</td>
<td></td>
</tr>
<tr>
<td>Lava lizards (8 populations of three <em>Tropidurus</em> spp.)</td>
<td>lizards on islands with introduced cats have higher FID</td>
<td>8 islands of the Galapagos</td>
<td>no mainland population</td>
<td>presence of exotic predators (cats)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>could be inherited, or learned</td>
<td>field observations; comparative analysis</td>
<td>[211]</td>
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<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
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<tr>
<td>Ibiza wall lizards ((Podarcis pityusensis))</td>
<td>FID and distance fled is greater on islets with higher predation pressure</td>
<td>7 islets around Ibiza and Formentera, Spain</td>
<td>no mainland population</td>
<td>predation pressure as estimated by number and kind of predators, incl. humans</td>
<td>unknown, both phenotypic plasticity and evolutionary processes deemed possible</td>
<td>field observations; comparative analysis</td>
<td>[212]</td>
</tr>
<tr>
<td>Lilford's wall lizard ((Podarcis lilfordi))</td>
<td>FID, distance fled, hiding time and probability to enter refuge are lower on islet with less predators</td>
<td>Islets of Rei and Aire (Menorca, Spain)</td>
<td>no mainland population</td>
<td>predation pressure</td>
<td>natural selection</td>
<td>Field observations</td>
<td>[213]</td>
</tr>
<tr>
<td>Italian wall lizard ((Podarcis siculus))</td>
<td>FID is shorter on island with lower predation pressure</td>
<td>comparison between two islands in the Adriatic Sea</td>
<td>no mainland population</td>
<td>predation pressure, through number of predators and habitat structure</td>
<td>unknown</td>
<td>field observations</td>
<td>[214]</td>
</tr>
<tr>
<td>66 lizard species</td>
<td>FID decreases as distance to mainland increases</td>
<td>islands in the Atlantic and Pacific Oceans; Caribbean and Mediterranean Seas</td>
<td>5 continents</td>
<td>predation pressure is lower on islands; reduced food availability may shorten FID to save energy</td>
<td>probably genetic changes, but tameness might be learned every generation</td>
<td>field observations; comparative analysis</td>
<td>[215]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
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<tr>
<td>Aegean wall lizard &lt;i&gt;(Podarcis erhardii)&lt;/i&gt;</td>
<td>lizards from islets have shorter FID and act bolder than lizards from main island</td>
<td>4 satellite islands of Naxos, Greece</td>
<td>18 populations on Naxos, Greece</td>
<td>cat predation</td>
<td>phenotypic plasticity; which is also maintained on islets</td>
<td>field observations; lab experiments</td>
<td>[216]</td>
</tr>
<tr>
<td>38 populations of Aegean wall lizards &lt;i&gt;(Podarcis erhardii)&lt;/i&gt;</td>
<td>lizards from smaller and more isolated islets have shorter FIDs</td>
<td>37 Cycladic islands</td>
<td>mainland Greece</td>
<td>predation</td>
<td>natural selection</td>
<td>field observations</td>
<td>[217]</td>
</tr>
<tr>
<td>Lilford's wall lizard &lt;i&gt;(Podarcis lilfordi)&lt;/i&gt;</td>
<td>FID and distance fled is not correlated with predation pressure</td>
<td>9 islets around Menorca and Mallorca, Spain</td>
<td>no mainland population</td>
<td>predation pressure as estimated by number and kind of predators, incl. humans</td>
<td>unknown, both phenotypic plasticity and evolutionary processes deemed possible</td>
<td>field observations; comparative analysis</td>
<td>[212]</td>
</tr>
<tr>
<td>Dalmatian wall lizard &lt;i&gt;(Podarcis melisellensis)&lt;/i&gt;</td>
<td>islet lizards are bolder, less wary but not less neophobic than island lizards</td>
<td>3 small islets out of the coast of Vis, Croatia</td>
<td>Vis, Croatia</td>
<td>food availability, predation pressure smaller on islets</td>
<td>plasticity or non-random gene-flow are suggested</td>
<td>field experiments</td>
<td>[218]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
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<tr>
<td>Common frog (<em>Rana temporaria</em>)</td>
<td>enhanced boldness and exploration in island tadpoles and froglets</td>
<td>4 islands in the Gulf of Bothnia, Sweden</td>
<td>Sweden</td>
<td>dispersal propensity; unstable conditions on islands (pond drying); reduced predation on islands</td>
<td>founder effects caused by environmental filtering or differential natural selection</td>
<td>lab experiments with wild-caught specimen; personality variation and behavioural syndrome measured</td>
<td>[57]</td>
</tr>
<tr>
<td>House mice (<em>Mus musculus domesticus</em>)</td>
<td>enhanced boldness and exploration on island</td>
<td>Gough Island</td>
<td>Maryland, US</td>
<td>novel food source (sea birds), loss of predatory danger, removal of human commensals, variable food availability</td>
<td>genetic change</td>
<td>common garden experiment with F1-offspring</td>
<td>[56]</td>
</tr>
<tr>
<td>61 species of parrots (Psittacidae)</td>
<td>Island species explore novel objects faster and longer than mainland species; island species are not less neophobic than mainland species.</td>
<td>several, not specified</td>
<td>several sites, not specified</td>
<td>assumed genetic</td>
<td>behavioral syndrome across species tested, but not at the individual level, or between island and mainland species</td>
<td>comparative analysis; behavioral syndrome across species tested, but not at the individual level, or between island and mainland species</td>
<td>[59]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
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<td>Type of analysis</td>
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<tr>
<td>Island scrub jays</td>
<td>island birds were more explorative than mainland birds</td>
<td>Santa Cruz Island, California, USA</td>
<td>mainland California, USA</td>
<td>reduced predation, more frequent food shortage on island</td>
<td>unknown</td>
<td>field/observations/experiments</td>
<td>[60]</td>
</tr>
<tr>
<td>(Aphelocoma insularis) vs California scrub jay (A. californica)</td>
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<tr>
<td>Brown anoles (Anolis sagrei)</td>
<td>lizards on islands with introduced predators are less explorative</td>
<td>8 small islands in the Caribbean, on four of which predatory lizards were introduced</td>
<td>no mainland population</td>
<td>presence of introduced predators (lizards)</td>
<td>natural selection</td>
<td>fitness gradient analysis; personality variation measured</td>
<td>[58]</td>
</tr>
<tr>
<td>Red-backed vole (Myodes gapperi)</td>
<td>island voles are less aggressive than mainland voles; no difference in exploration</td>
<td>10 islands in the Winnipeg River, Ontario, Canada</td>
<td>6 sites on mainland Ontario</td>
<td>relaxed predation, higher population density</td>
<td>dispersal-related, ecological and evolutionary mechanisms all considered</td>
<td>lab experiment; comparative analysis</td>
<td>[62]</td>
</tr>
<tr>
<td>Deer mice (Peromyscus maniculatus)</td>
<td>wild-caught island mice are less aggressive, but difference disappears in subsequent generations</td>
<td>Saturna Island, Pender Island, British Columbia, Canada</td>
<td>population density thought to reduce aggressiveness</td>
<td>phenotypic plasticity</td>
<td></td>
<td>lab experiment with wild-caught specimen and their offspring; crossings</td>
<td>[67]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
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<tr>
<td>Deer mice <em>(Peromyscus maniculatus)</em></td>
<td>island mice do not show aggressive behaviour towards juveniles; some mainland mice behave aggressively towards non-kin.</td>
<td>Saturna Island, British Columbia, Canada</td>
<td>Saturna Island, British Columbia, Canada</td>
<td>reduced intraspecific competition due to high food supply on island</td>
<td>Unknown</td>
<td>lab test on P (interact with F1)</td>
<td>[68]</td>
</tr>
<tr>
<td>Common shrew <em>(Sorex araneus)</em></td>
<td>island and mainland shrews equally aggressive</td>
<td>4 islands in the Baltic Sea</td>
<td>2 sites on mainland Finland</td>
<td>island specimens often inbred</td>
<td>lab experiments with field-caught individuals</td>
<td>[219]</td>
<td></td>
</tr>
<tr>
<td>Skyros wall lizard <em>(Podarcis gaigeae)</em></td>
<td>islet lizards more likely to attack juveniles and behave more aggressively to other adults</td>
<td>islet Diavates</td>
<td>Skyros main island</td>
<td>food scarcity and high population size prompt for cannibalism</td>
<td>Unknown</td>
<td>lab experiments with field-caught individuals</td>
<td>[75]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
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<tr>
<td>Tiger snakes <em>(Notechis scutatus)</em></td>
<td>adult snakes from predator-rich sites have more vigorous responses when handled, but neonatal behaviour is unrelated to predator species richness</td>
<td>8 islands around Australia</td>
<td>3 sites, on mainland Australia and Tasmania</td>
<td>predation pressure, through number and type of predators</td>
<td>ontogenetic plasticity; experience, or genetically coded adjustment of behaviour to ontogenetically variable traits</td>
<td>observations on freshly caught individuals</td>
<td>[71,72]</td>
</tr>
<tr>
<td>Common garter snakes <em>(Thamnophis sirtalis)</em></td>
<td>adult but not neonate snakes from the mainland behave more aggressively towards experimenter than island snakes</td>
<td>Beaver Archipelago, USA</td>
<td>Michigan, USA</td>
<td>fewer predators on island</td>
<td>both innate and environmental influences</td>
<td>laboratory behavioural observations</td>
<td>[73]</td>
</tr>
<tr>
<td>Pacific rattlesnake <em>(Crotalus oreganus)</em></td>
<td>island snakes behave more aggressively towards humans</td>
<td>Santa Catalina Island, USA</td>
<td>mainland California, USA</td>
<td>island has fewer avian predators but perhaps more (introduced) mammalian predators</td>
<td>Unknown</td>
<td>field observations</td>
<td>[74]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
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<tr>
<td>Chuckwalla species</td>
<td>island endemics are more sociable, less aggressive than mainland</td>
<td>San Esteban Island and Angel Island, California, USA</td>
<td>mainland California, USA</td>
<td>dearth of predators, competitors, niche expansion, high but fluctuating food supply, high density on island</td>
<td>Unknown</td>
<td>field observations</td>
<td>[77]</td>
</tr>
<tr>
<td>(Sauromalus spp.)</td>
<td>species</td>
<td></td>
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<tr>
<td>House mice (Mus</td>
<td>island mice do not show aggressive, defensive or cautious behaviour</td>
<td>Isle of May, UK</td>
<td>Nottinghamshire, UK</td>
<td>interaction between resource distribution, habitat structure and predation risk</td>
<td>Unknown</td>
<td>lab experiments on recently caught specimens</td>
<td>[69]</td>
</tr>
<tr>
<td>musculus domesticus)</td>
<td>towards conspecifics</td>
<td></td>
<td></td>
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<tr>
<td>Yellow-faced grass-</td>
<td>island birds are more territorial than mainland birds, which</td>
<td>Jamaica</td>
<td>Costa Rica</td>
<td>island density is lower</td>
<td>Unknown</td>
<td>field observations</td>
<td>[78]</td>
</tr>
<tr>
<td>quit (Tiaris olivacea)</td>
<td>occur more often in flocks</td>
<td></td>
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<td>Study species</td>
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<td>Island</td>
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<tr>
<td>Human (Homo sapiens)</td>
<td>islanders exhibit greater animosity towards strangers and keep greater social distance</td>
<td>Croatian Islands</td>
<td>mainland Croatia</td>
<td>dangers associated with infectious disease</td>
<td></td>
<td>Questionnaire</td>
<td>[81]</td>
</tr>
<tr>
<td>Human (Homo sapiens)</td>
<td>islanders had higher levels of consciousness, emotional stability and lower levels of extraversion and openness; no difference in agreeableness</td>
<td>Giglio, Ponza and Ventotene, and seven Aeolian islands, Italy</td>
<td>3 sites on mainland Italy</td>
<td>island is harsh, restricted environment with limited social environment</td>
<td>assumed adaptive (changes in same direction); elimination of well less adapted through mortality, assortative mating or emigration</td>
<td>Questionnaire</td>
<td>[63-65]</td>
</tr>
<tr>
<td>Meadow voles (Microtus pennsylvanicus) versus beach voles (M. breweri)</td>
<td>island species is more sociable</td>
<td>Muskeget Island, Massachusetts, USA</td>
<td>mainland Massachusetts, USA</td>
<td>differential dispersal of intolerant specimens</td>
<td></td>
<td>field observations</td>
<td>[76]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
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<tr>
<td>46 species of birds</td>
<td>birds on islands tend to flock less than birds on the mainland</td>
<td>22 different islands</td>
<td>22 mainland sites to match islands</td>
<td>predation pressure</td>
<td>random drift or active selection are suggested</td>
<td>comparative analysis</td>
<td>[79]</td>
</tr>
<tr>
<td>Long-tailed macaques (Macaca fascicularis)</td>
<td>smaller group sizes on island time allocation is dependent on group size on mainland and islands with reduced number of predators, but not on predator-free island</td>
<td>Simeulue, Indonesia, Sumatra, Indonesia</td>
<td>felid predation</td>
<td>absence of predators</td>
<td>unknown</td>
<td>field observations</td>
<td>[80]</td>
</tr>
<tr>
<td>Tammar wallabies (Macropus eugenii)</td>
<td></td>
<td>Simeulue, Indonesia, Sumatra, Indonesia</td>
<td>Western Australia</td>
<td></td>
<td>maintained by natural selection, but 'priming agents' may be required to develop antipredator behaviour</td>
<td>field observations</td>
<td>[206]</td>
</tr>
<tr>
<td>Oriental fire-bellied toads (Bombina orientalis)</td>
<td>island toads have lower levels of activity</td>
<td>Jeju Island, South Korea</td>
<td>2 sites on mainland South Korea</td>
<td>predation is higher on island</td>
<td>local selection, founder effects also considered possible</td>
<td>lab observations</td>
<td>[83]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
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<tr>
<td>Clouded anoles (&lt;i&gt;Anolis nebulosus&lt;/i&gt;)</td>
<td>island anoles are more active</td>
<td>San Agustín, México</td>
<td>mainland México</td>
<td>less variable environmental conditions on island may allow better thermoregulation; higher predation on mainland</td>
<td>field observations</td>
<td>[82]</td>
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</tbody>
</table>

**Cognition**

<table>
<thead>
<tr>
<th>Minatogawa man (&lt;i&gt;Homo sapiens&lt;/i&gt;) versus modern Japanese and Pleistocene/Holocene H. sapiens.</th>
<th>Pleistocene island dwellers had relatively small endocrania</th>
<th>Okinawa Island, Japan</th>
<th>mainland Japan</th>
<th>undernutrition</th>
<th>phenotypic plasticity; genetic adaptation</th>
<th>comparative analysis of brain size</th>
<th>[220]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human (&lt;i&gt;Homo floresiensis&lt;/i&gt; versus &lt;i&gt;Homo erectus&lt;/i&gt;)</td>
<td>relative brain size is lower in island species</td>
<td>Flores, Indonesia</td>
<td>main area Japan</td>
<td>biotic interactions and resource use</td>
<td>natural selection for smaller brains (in addition to selection for smaller body size).</td>
<td>quantitative genetic modelling</td>
<td>[221]</td>
</tr>
<tr>
<td>Mouse and dwarf lemurs (&lt;i&gt;Cheirogaleidae&lt;/i&gt;)</td>
<td>disproportional reduction in brain size in this island clade</td>
<td>Madagascar</td>
<td>main area</td>
<td>unpredictable food availability</td>
<td>natural selection</td>
<td>comparative analysis of brain size</td>
<td>[222]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
<td>Driver</td>
<td>Mechanism</td>
<td>Type of analysis</td>
<td>Reference</td>
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<tr>
<td>Malagasy dwarf hippos (Hippopotamus lemerlei, H. madagascariensis) versus hippopotamus (H. amphibius)</td>
<td>relative brain size is lower in island species</td>
<td>Madagascar</td>
<td>mainland Africa</td>
<td>poor dietary resources on islands</td>
<td>natural selection for smaller brains (in addition to selection for smaller body size).</td>
<td>ontogenetic modelling</td>
<td>[85]</td>
</tr>
<tr>
<td>Siculo-Maltese dwarf elephant (Palaeoloxodon falconeri) versus P. antiquus</td>
<td>relative brain size is lower in island species</td>
<td>Malta</td>
<td>mainland Africa</td>
<td>poor dietary resources on islands</td>
<td>natural selection for smaller brains (in addition to selection for smaller body size).</td>
<td>ontogenetic modelling</td>
<td>[85]</td>
</tr>
<tr>
<td>Siculo-Maltese dwarf elephant (Palaeoloxodon falconeri) versus P. antiquus</td>
<td>dwarfed insular species has a high encephalization quotient</td>
<td>Sicily, Italy</td>
<td>mainland Europe</td>
<td>need to maintain the minimal functional volume of the brain when the size of the skull was drastically reduced</td>
<td>allometric analysis</td>
<td>[86]</td>
<td></td>
</tr>
<tr>
<td>Study species</td>
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<tr>
<td>Balearic Islands cave goat (<em>Myotragus</em> spp.) compared to 54 spp. of extant bovids</td>
<td>insular species have small brain and sense organs relative to body size</td>
<td>Balearic Islands, Spain</td>
<td>mainland Africa</td>
<td>absence of predators; overpopulation; limited energy availability</td>
<td>natural selection for smaller brains (in addition to selection for smaller body size)</td>
<td>scaling analysis</td>
<td>[223]</td>
</tr>
<tr>
<td>Cretan deer (<em>Candiacervus</em>), compared to extant deer (Cervidae)</td>
<td>insular dwarf deer have normal relative brain size</td>
<td>Crete, Greece</td>
<td></td>
<td>dearth of predators on islands</td>
<td></td>
<td>comparative analysis of brain size</td>
<td>[87]</td>
</tr>
<tr>
<td>Sardinian dhole (<em>Cynotherium sardous</em>), compared to 2 spp of extant dog spp. (Canidae)</td>
<td>insular dwarf canid has normal relative brain size</td>
<td>Sardinia, Italy</td>
<td></td>
<td></td>
<td></td>
<td>comparative analysis of brain size</td>
<td>[88]</td>
</tr>
<tr>
<td>Minorcan giant rabbit (<em>Nuralagus rex</em>), compared to extant rabbit species (Leporidae)</td>
<td>Late neogene insular giant had relatively small brain; especially sense-dependent areas are small</td>
<td>Minorca, Balearic Islands, Spain</td>
<td></td>
<td>absence of predators; limited energy availability</td>
<td></td>
<td>comparative analysis of brain size</td>
<td>[224]</td>
</tr>
<tr>
<td>426 mammalian species</td>
<td>no effect of insularity on relative brain size</td>
<td>islands worldwide</td>
<td>mainland sites throughout the world</td>
<td>poor dietary resources on islands</td>
<td>natural selection for smaller brains</td>
<td>comparative analysis of brain size</td>
<td>[90]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
<td>Island</td>
<td>Mainland</td>
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<tr>
<td>Dodo (Raphus cucullatus) compared to 9 spp of pigeons (Columbiformes)</td>
<td>endocranial volume not smaller than expected from pigeon-allometry</td>
<td>Mauritius</td>
<td></td>
<td></td>
<td></td>
<td>allometric analysis</td>
<td>[89]</td>
</tr>
<tr>
<td>Rodrigues Island giant owl (Otus murivorus), compared to 10 extant spp. Owls (Strigidae)</td>
<td>reduction of brain volume in extinct island endemic</td>
<td>Rodrigues, Mauritius</td>
<td>diverse</td>
<td>absence of predators, reduction of interspecific competition</td>
<td>brain expansion cannot follow pace of body size increase ('evolutionary pace dissociation')</td>
<td>comparative analysis of brain size</td>
<td>[225]</td>
</tr>
<tr>
<td>Haast’s eagle (Harpagornis moorei), compared to 35 spp of eagles (Accipitridae)</td>
<td>island endemic had low endocranial volume for its body mass</td>
<td>New Zealand</td>
<td>diverse</td>
<td>absence of predators, competitors on island</td>
<td>mismatch between neural and somatic growth</td>
<td>comparative analysis of brain size</td>
<td>[226]</td>
</tr>
<tr>
<td>40 Crow and raven species (Corvus)</td>
<td>brain size does not predict ability to colonize islands</td>
<td>islands worldwide</td>
<td>mainland sites throughout the world</td>
<td>islands are challenging environments, promoting enhanced cognition</td>
<td></td>
<td>comparative analysis of brain size</td>
<td>[91]</td>
</tr>
<tr>
<td>Study species</td>
<td>Trait</td>
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</tr>
<tr>
<td>&gt;1900 species of birds</td>
<td>insular species have larger brains</td>
<td>diverse</td>
<td>diverse</td>
<td>high environmental unpredictability across years</td>
<td>natural selection; high phenotypic plasticity may inhibit evolutionary change in some clades</td>
<td>comparative analysis of brain size</td>
<td>[92]</td>
</tr>
</tbody>
</table>
**Table 2:** — Outstanding questions on the evolution of personality and cognition on islands

**THE MASTER DATA**

<table>
<thead>
<tr>
<th>Question</th>
<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>Do island populations exhibit repeatable inter-individual differences in the way they behaviourally interact with their environment, and are these differences consistent across contexts?</td>
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</tr>
<tr>
<td>Do populations (or communities) on islands exhibit the same range and relative frequencies of behavioural types as populations on the mainland, or on other islands?</td>
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</tr>
<tr>
<td>Do animal populations on islands differ in cognitive skills from their counterparts on the mainland, or on other islands?</td>
<td>Do animal populations on islands differ in cognitive skills from their counterparts on the mainland, or on other islands?</td>
</tr>
</tbody>
</table>

**THE MECHANISMS OF CHANGE**

<table>
<thead>
<tr>
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<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>What is the role of non-adaptive evolution (e.g. inbreeding, genetic drift, pleiotropy) in creating differences in cognition and personality between island and mainland populations?</td>
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</tr>
<tr>
<td>What is the role of dispersal filtering in creating differences in cognition and personality between island and mainland populations? How long does this effect linger?</td>
<td>What is the role of dispersal filtering in creating differences in cognition and personality between island and mainland populations? How long does this effect linger?</td>
</tr>
<tr>
<td>What is the role of phenotypic plasticity versus genetic adaptation in creating differences in cognition and personality between island and mainland populations?</td>
<td>What is the role of phenotypic plasticity versus genetic adaptation in creating differences in cognition and personality between island and mainland populations?</td>
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</table>

**THE DRIVERS OF CHANGE**

<table>
<thead>
<tr>
<th>Question</th>
<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>What is the effect of predator release on islands on personality traits? Are these effects general, or specific to a predatory context?</td>
<td>What is the effect of predator release on islands on personality traits? Are these effects general, or specific to a predatory context?</td>
</tr>
<tr>
<td>Does predator release on islands affect prey cognitive capacity? (How fast) do prey species lose their ability to recognize predators, to respond in adequate ways? Are these effects general, or specific to a predatory context?</td>
<td>Does predator release on islands affect prey cognitive capacity? (How fast) do prey species lose their ability to recognize predators, to respond in adequate ways? Are these effects general, or specific to a predatory context?</td>
</tr>
</tbody>
</table>
How does reduced interspecific competition (and the possible resulting niche shift) on islands affect personality traits? Are these effects general, or specific to an interspecific context?

How do high population densities on islands affect personality?

How does low resource availability or predictability affect personality traits, and cognitive capacity?

COVARIATION WITH OTHER CHARACTERISTICS

Do changes in morphology (e.g. body size, shape, colour), physiology (e.g. brain size, digestive performance) or diet (type or breadth) observed in island populations concur with changes in personal or cognitive capacity? Are these changes adaptive or constrained?

Do changes in life history of the pace of life (fast to slow) on islands affect personality and cognition?

GENERALITY AND RELEVANCE

Are the magnitude and the direction of changes in personality and cognitive traits on islands consistent over taxonomic groups and island environments? If not, which factors are responsible?

How do personality and cognitive characteristics of island populations affect their vulnerability to alien species? How readily can island animals adjust personality and cognitive traits to cope with new challenges?