How to behave when marooned: The behavioural component of the island syndrome remains underexplored

Ioanna Gavriilidi[1,*], Gilles De Meester[1], Raoul Van Damme[1] & Simon Baeckens[1,2]

[1] Functional Morphology Lab, Department of Biology, University of Antwerp, Wilrijk, Belgium.
[2] Evolution and Optics of Nanostructures Lab, Department of Biology, Ghent University, Ghent, Belgium

Review

[*]**Corresponding author:** ioanna.gavriilidi@uantwerp.be

Funding: — Financial support was given by the University of Antwerp (IG, RVD) and the Research Foundation-Flanders (FWO) (IG: 1105122N; GDM: 1144118N; SB: 12I8822N).

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.

References

1. Adler GH, Levins R. 1994 The island syndrome in rodent populations. *Q. Rev. Biol.* **69**, 473-490. (doi:10.1007/bf00329044)
2. Baeckens S, Van Damme R. 2020 The island syndrome. *Curr. Biol.* **30**, 338-339.
3. Burns KC. 2019 *Evolution in Isolation: The Search for an Island Syndrome in Plants.* Cambridge: Cambridge Univ Press.
4. Whittaker RJ, Fernández-Palacios JM. 2006. *Island biogeography; ecology, evolution and conservation.* Oxford, UK: Oxford University Press. (doi:10.1046/j.1365-2745.2000.00425.x)
5. Losos JB, Ricklefs RE. 2009 Adaptation and diversification on islands. *Nature* **457**, 830-836. (doi:10.1038/nature07893)
6. Covas, R. 2012 Evolution of reproductive life histories in island birds worldwide. *Proc. R. Soc. B - Biol. Sci.*, **279**, 1531-1537. (doi:10.1098/rspb.2011.1785)
7. Doutrelant, C., Paquet, M., Renoult, J. P., Grégoire, A., Crochet, P. A., & Covas, R. 2016 Worldwide patterns of bird colouration on islands. *Ecol. Lett.* **19**, 537-545. (doi: 10.1111/ele.12588)
8. Darwin C. 1839 Journal of researches into the geology and natural history of the various countries visited by H. M. S. Beagle, under the command of captain Fitzroy, R. N. from 1832 – 1836. London, UK: Henry Colburn.
9. Cooper WE Jr, Pyron RA, Garland T Jr. 2014 Island tameness: living on islands reduces flight initiation distance. *Proc. R. Soc. - Biol. Sci.* **281**, 20133019. (doi: 10.1098/rspb.2013.3019)
10. Dougherty LR, Guillette LM 2018 Linking personality and cognition: a meta-analysis. *Phil. Trans. R. Soc. B – Biol. Sci.* **373,** 1756. (doi: 10.1098/rstb.2017.0282)
11. MacArthur RH, Wilson EO. 1967 *The theory of island biogeography*. Princeton, NJ: Princeton Univ Press. (doi: 10.1515/9781400881376)
12. Lack D. 1969 The number of bird species on islands. *Bird Study* **16**, 193-209. (doi: 10.1080/00063656909476244)
13. Cox GW, Ricklefs RE. 1977 Species diversity, ecological release, and community structuring in Caribbean land bird faunas. *Oikos* **28**, 113-122. (doi.org/10.2307/3543330)
14. Herrmann NC, Stroud JT, Losos JB. 2021 The Evolution of 'Ecological Release' into the 21st Century. *Trends Ecol. Evol.* **36**, 206–215. (doi.org/10.1016/j.tree.2020.10.019)

15. MacArthur RH, Diamond JM, Karr JR. 1972 Density compensation in island faunas. *Ecology* **53**, 330-342. (doi: 10.2307/1934090)

16. Case TJ, Gilpin ME, Diamond JM. 1979 Overexploitation, interference competition, and excess density compensation in insular faunas. *Am. Nat.* **113**, 843-854. (doi: 10.1086/283440)

17. Buckley LB, Jetz W. 2007 Insularity and the determinants of lizard population density. *Ecol. Lett.* **10**, 481-489. (doi: 10.1111/j.1461-0248.2007.01042.x)

18. Janzen D. 1973 Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. *Ecology* **54**, 659-686. (doi: 10.2307/1935358)

19. Blanco G, Laiolo P, Fargallo JA. 2014 Linking environmental stress, feeding-shifts and the 'island syndrome': a nutritional challenge hypothesis. *Popul. Ecol.* **56,** 203–216 (doi: 10.1007/s10144-013-0404-3)

20. Andrews RM. 1979 Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. *Brevoria* **454**, 1-51. (doi: 10.1111/j.1365-2699.2010.02466.x)

21. Olesen JM, Valido A. 2003 Lizards as pollinators and seed dispersers: an island phenomenon. *Trends Ecol. Evol.* **18**, 177-181. (doi: 10.1016/s0169-5347(03)00004-1)

22. Dochtermann, N. A., Schwab, T., & Sih, A. 2015 The contribution of additive genetic variation to personality variation: heritability of personality. *Proc. R. Soc. B - Biol. Sci.* **282**, 20142201. (doi: 10.1098/rspb.2014.2201)

23. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291-318. (doi: 10.1111/j.1469-185x.2007.00010.x)

24. Sih A, Bell AM, Johnson JC, Ziemba RE. 2004 Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **79**, 241-277. (doi: 10.1086/422893)

25. Dukas, R. 2004 Evolutionary biology of animal cognition. *Annu. Rev. Ecol. Evol. Syst.* **35**, 347-374. (doi: 10.1146/annurev.ecolsys.35.112202.130152)

26. Huebner, F., Fichtel, C., & Kappeler, P. M. 2018 Linking cognition with fitness in a wild primate: fitness correlates of problem-solving performance and spatial learning ability. *Phil. Trans. R. Soc. B* **373**, 20170295. (doi: 10.1098/rstb.2017.0295)

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

mated to males with better spatial cognition. *Ecol. Lett.* **22**, 897-903. (doi: 10.1111/ele.13249)

28. Sonnenberg BR, Branch CL, Pitera AM, Bridge E, Pravosudov VV 2019 Natural selection and spatial cognition in wild food-caching mountain chickadees. *Curr. Biol.* **29**, 670-676. (doi: 10.1016/j.cub.2019.01.006)

29. Ashton BJ, Ridley AR, Edwards EK, Thornton A. 2018 Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature* **554**, 364-367. (doi: 10.1038/nature25503)

30. Cauchoix M, Chow PK, Van Horik JO, Atance CM, Barbeau EJ, Barragan-Jason G, Bize P, Boussard A, Buechel SD, Cabirol A, Cauchard L. 2018 The repeatability of cognitive performance: a meta-analysis. *Proc. R. Soc. B - Biol. Sci.* **373**, 20170281. (doi: 10.1098/rstb.2017.0281)

31. Griffin AS, Guillette LM, Healy SD. 2015 Cognition and personality: an analysis of an emerging field. *Trends Ecol. Evol.* **30**, 207-214. (doi: 10.1016/j.tree.2015.01.012)

32. Spearman C. 1904 General intelligence, objectively determined and measured. *Am. J. Psychol.* **15**, 201-292. (doi: 10.1037/11491-006)

33. Warne RT, Burningham C. 2019 Spearman’s g found in 31 non-Western nations: Strong evidence that g is a universal phenomenon. *Psych. Bull.* **145**, 237-272. (doi: 10.31234/osf.io/uv673)

34. Galsworthy MJ et al. 2005. Assessing reliability, heritability and general cognitive ability in a battery of cognitive tasks for laboratory mice. *Behav. Genet.* **35,** 675-692 (doi: 10.1007/s10519-005-3423-9)

35. Shaw RC et al. 2015. Wild psychometrics: Evidence for ‘general’ cognitive performance in wild New Zealand robins, *Petroica longipes*. *Anim. Behav.* **109,** 101–111 (doi: 10.1016/j.anbehav.2015.08.001)

36. Poirier MA et al. 2020. How general is cognitive ability in non-human animals? A meta-analytical and multi-level reanalysis approach. *Proc. R. Soc. - Biol. Sci* **287,** 20201853 (doi: 10.1098/rspb.2020.1853)

37. Etheridge R. 1889 The general zoology of Lord Howe Island; containing also an account of the collections made by the Australian Museum Collecting Party, Aug-Sept 1887. *Austral. Mus. Mem.* **2,** 1-42. (doi: 10.3853/j.0067-1967.2.1889.479)

38. Rothschildt W, Hartert E. 1899 A review of the ornithology of the Galapagos islands. With notes on the Webster-Harris expedition. *Novitates Zool.* **6**, 85-205.

39. Blumstein DT. 2002 Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *J. Biogeogr.* **29**, 685-692. (doi: 10.1046/j.1365-2699.2002.00717.x)

40. Reimers E, Lund S, Ergon T. 2011 Vigilance and fright behaviour in the insular Svalbard reindeer. *Can. J. Zool.* **89**, 753-764. (doi: 10.1139/z11-040)

41. Hamao S, Torikai H, Yoshikawa M, Yamamoto Y, Ijichi T. 2020 Risk-taking behavior of bull-headed shrikes that recently colonized islands. *Curr. Zool.* **67,** 177-182. (doi: 10.1093/cz/zoaa036)

42. Delibes MC, Blázques MC, Soriano E, Revilla E, Godoy JA. 2011 High antipredatory efficiency of insular lizards: a warning signal of excessive specimen collection? *Plos One* **6**, e29312. (doi: 10.1371/journal.pone.0029312)

43. Zuberogoitia I, Martínez JE, Margalida A, Gómez I, Azkona A, Martínez JA. 2010 Reduced food availability induces behavioural changes in Griffon vulture *Gyps fulvus*. *Ornis Fenn.* **87**, 52-60.

44. Bauwens D, Thoen C. 1981 Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara. J. Anim. Ecol.* **50**, 733-743. (doi: 10.2307/4133)

45. Seltmann MW, Öst M, Jaatinen K, Atkinson S, Mashburn K, Hollmén T. 2012 Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Anim. Behav.* **84**, 889-896. (doi: 10.1016/j.anbehav.2012.07.012)

46. Rocha C, Bergallo H. 1990 Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. *Ethol. Ecol. Evol.* **2**, 263-268. (doi: 10.1016/j.anbehav.2012.07.012)

47. Capizzi D, Luiselli L, Viguoli L. 2007 Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition in two lacertids with contrasting habits. *Amphibia-Reptilia* **28**, 403-407. (doi: 10.1163/156853807781374827)

48. Engelhardt SC, Weladii RB. 2011 Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Can. J. Zool.* **89**, 823-830. (doi: doi.org/10.1139/z11-054)

49. Cooper WE Jr. 2009 Flight initiation distance during social activity in lizards (*Sceloporus virgatus*). *Behav. Ecol. Sociobiol.* **63**, 1765-1771. (doi: 10.1007/s00265-009-0799-1)

50. Dill LM, Houtman R. 1989 The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Can. J. Zool.* **67,** 233-235. (doi: 10.1139/z89-033)

51. Wilson D.S. et al. 1994. Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9,** 442–446 (doi: 10.1016/0169-5347(94)90134-1)

52. Dingemanse NJ, Reale D. 2005. Natural selection and animal personality. *Behaviour* **142,** 1159–1184 (doi: 10.1163/156853905774539445)

53. Polis GA, Hurd SD 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proc. Natl. Acad. Sci. USA* **92**, 4382-4386 (doi: 10.2307/2367331)

54. Novosolov M et al. 2016. Power in numbers. Drivers of high population density in insular lizards. *Global Ecol. Biogeogr*. **25,** 87-95 (doi: 10.1111/geb.12390)

55. Burns KC 2021. An anecdotal observation of anti-predatory tool use in a New Zealand parrot. *Behaviour* **1(aop),** 1-7 (doi: 10.1163/1568539X-bja10137)

56. Stratton JA, Nolte MJ, Payseur BA. 2021 Evolution of boldness and exploratory behavior in giant mice from Gough Island. *Behav. Ecol. Sociobiol.* **75**, 65. (doi: 10.1101/2020.09.10.292185)

57. Brodin T, Lind MI, Wiberg MK, Johansson F. 2013 Personality trait differences between mainland and island populations in the common frog (*Rana temporaria*). *Behav. Ecol. Sociobiol.* **67,** 135-143. (doi: 10.1007/s00265-012-1433-1)

58. Lapiedra O, Schoener TW, Leal M, Losos JB, Kolbe JJ. 2018 Predator-driven natural selection on risk-taking behavior in anole lizards. *Science* **360**, 1017-1020. (doi: 10.1126/science.aap9289)

59. Mettke-Hofmann C, Winkler H, Leisler B. 2002 The significance of ecological factors for exploration and neophobia in parrots. *Ethology* **108**, 249-272. (doi: 10.1046/j.1439-0310.2002.00773.x)

60. Haemig PD. 1988 A comparative experimental study of exploratory behaviour in Santa Cruz Island and mainland California scrub jays *Aphelocoma coerulescens*. *Bird Behav.* **8,** 38-42. (doi: 10.3727/015613888791871296)

61. Mettke-Hofmann, C. 2014 Cognitive ecology: ecological factors, life-styles, and cognition. *Wiley Interdiscip. Rev. Cogn. Sci.* **5**, 345-360. (doi: 10.1002/wcs.1289)

62. Juette T, Garant D, Jameson JW, Réale D. 2020 The island syndrome hypothesis is only partially validated in two rodent species in an inland–island system. *Oikos* **129**, 1739-1751. (doi: 10.1111/oik.07249)

63. Camperio Ciani AS, Capiluppi C. 2011 Gene flow by selective emigration as a possible cause for personality differences between small islands and mainland populations. *Eur. J. Personality* **25,** 53-64. (doi: 10.1002/per.774)

64. Camperio Ciani AS, Capiluppi C, Veronese A, Sartori G. 2007 The adaptive value of personality differences revealed by small island population dynamics. *Eur. J. Personality* **21,** 3-22. (doi: 10.1002/per.595)

65. Camperio Ciani AS, Edelman S, Ebstein RP. 2013 The Dopamine D4 Receptor (DRD4) Exon 3 VNTR contributes to adaptive personality differences in an Italian small island population. *Eur. J. Personality* **27**, 593-604. (doi: 10.1002/per.1917)

66. Stamps JA, Buechner M 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *Quart. Rev. Biol.* **60,** 155-181. (doi: 10.1086/414314)

67. Baier F, Hoekstra HE. 2019 The genetics of morphological and behavioural island traits in deer mice. *Proc. Royal Soc. B-Biol. Sci.* **286**, 20191697. (doi: 10.1101/443432)

68. Halpin ZT. 1981 Adult-young interactions in island and mainland populations of the deer mouse *Peromyscus maniculatus*. *Oecologia* **51**, 419-425. (doi: 10.1007/bf00540916)

69. Gray S, Hurst J. 1998 Competitive behaviour in an island population of house mice, *Mus domesticus*. *Anim. Behav.* **56,** 1291-1299. (doi: 10.1006/anbe.1998.0890)

70. Morinay, J., Cardoso, G. C., Doutrelant, C., & Covas, R. 2013 The evolution of birdsong on islands. *Ecol. Evol.* **3**, 5127-5140 (doi: 10.1002/ece3.864)

71. Bonnet X, Aubret F, Lourdais O, Ladyman M, Bradshaw SD, Maumelat S. 2005 Do 'quiet' places make animals placid? Island versus mainland tiger snakes. *Ethology* **111**, 573-592. (doi: 10.1111/j.1439-0310.2005.01070.x)

72. Aubret F, Michniewicz RJ, Shine R. 2011 Correlated geographic variation in predation risk and antipredator behaviour within a wide-ranging snake species (*Notechis scutatus*, Elapidae). *Austral Ecol.* **36**, 446-452. (doi: 10.1111/j.1442-9993.2010.02171.x)

73. Placyck JS Jr. 2012 The role of innate and environmental influences in shaping antipredator behavior of mainland and insular garter snakes (*Thamnophis sirtalis*). *J. Ethol.* **30**, 101-108. (doi: 10.1007/s10164-011-0302-0)

74. Person CE, Fox GA, King J, Gren ECK, Briggs E, Hayes WK. 2006 Paradoxical exception to island tameness: increased defensiveness in an insular population of rattlesnakes. *Toxicon* **119**, 375-376. (doi: 10.1016/j.toxicon.2016.06.038)

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)

76. Reich LM, Tamarin RH. 1980 Trap use as an indicator of social behavior in mainland and island voles. *Acta Theriologica* **25,** 295-307. (doi: 10.4098/at.arch.80-26)

77. Case TJ. 1982 Ecology and evolution of the insular gigantic chuckawallas, *Sauromalus hispidus* and *Sauromalus varius*. In *Iguanas of the world. Their behavior, ecology and conservation* (eds Burghardt GM, Rand AS). Park Ridge, NJ: Noyes Publ. (doi: 10.2307/2829735)

78. Pulliam HR. 1973 Comparative feeding ecology of a tropical grassland finch (*Tiaris olivacea*). *Ecology* **54**, 284-299. (doi: 10.2307/1934337)

79. Beauchamp G. 2004 Reduced flocking by birds on islands with relaxed predation. *Proc. Royal Soc. B-Biol. Sci.* **271**, 1039-1042. (doi: 10.1098/rspb.2004.2703)

80. van Schaik CP, van Noordwijk MA. 1985 Evolutionary effect of the absence of felids on the social organization of the macaques on the Island of Simeulue (*Macaca fascicularis fusca*, Miller 1903). *Folia Primatol.* **44**, 138-147. (doi: 10.1159/000156208)

81. Hromatko I, Grus A, Kolđeraj G. 2021 Do islanders have a more reactive behavioral immune system? Social cognitions and preferred interpersonal distances during the COVID-19 pandemic. *Frontiers Psychol*. **12,** 2021.647586. (doi: 10.3389/fpsyg.2021.647586)

82. Siliceo-Cantero & García A. 2015 Actividad y uso del hábitat de una población insular y una continental de lagartijas *Anolis nebulosus* (Squamata: Polychrotidae) en un ambiente estacional. *Rev. Mex. Biodiv.* **86**, 406-411. (doi: 10.1016/j.rmb.2015.04.011)

83. Kang C, Sherratt TN, Kim YE, Shin Y, Moon J, Song U, Kang JY, Kim K, Jang Y. 2017 Differential predation drives the geographical divergence in multiple traits in aposematic frogs. *Behav. Ecol.* **28**, 1122-1130. (doi: 10.1093/beheco/arx076)

84. Killen SS, Calsbeek R, Williams TD. 2017 The ecology of exercise: mechanisms underlying individual variation in behavior, activity, and performance. *Integr. Comp. Biol.* **57**, 185-194. (doi: 10.1093/icb/icx083)

85. Weston EM, Lister AM 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature* **459**, 85-88. (doi: 10.1038/nature07922)

86. Larramendi A, Palombo MR 2015. Body size, biology and encephalization quotient of *Palaeoloxodon* ex gr. *P. falconeri* from Spinagallo cave (Hyblean plateau, Sicily). *Hystrix* **26**, 1-8. (doi: 10.4404/hystrix-26.2-11478)

87. Palombo MR, Köhler M, Moya Sola S, Giovinazzo C. 2008 Brain versus body mass in endemic ruminant artiodactyls: A case studied of *Myotragus balearicus* and smallest *Candiacervus* species from Mediterranean Islands. *Quaternary Internat.* **182**, 160-183. (doi: 10.1016/j.quaint.2007.08.037)

88. Palombo MR, Giovanazzo C. 2004 Brain weight versus body mass in late Pleistocene *Cynotherium sardous* Studiati, 1847 from Dragonara Cave (north-western Sardinia). *Giornate Paleontol.* **4,** 44.

89. Gold MEL, Bourdon E, Norell MA. 2016 The first endocast of the extinct dodo (*Raphus cucullatus*) and an anatomical comparison amongst close relatives (Aves, Columbiformes). *Zool. J. Linn. Soc.* **177,** 950-963. (doi: 10.1111/zoj.12388)

90. Castiglione S, Serio C, Piccolo M, Mondanaro A, Melchionna M, Di Febbraro M, Sansalone G, Wroe S, Raia P. 2021 The influence of domestication, insularity and sociality on the tempo and mode of brain size evolution in mammals. *Biol. J. Linn. Soc.* **132,** 221-231. (doi: 10.1093/biolinnean/blaa186)

91. Jønsson KA, Fabre PH, Irestedt M. 2013 Brains, tools, innovation and biogeography in crows and ravens. *BMC Evol. Biol.* **12**, 72. (doi: 10.1671/039.029.0325)

92. Sayol F, Downing PA, Iwaniuk AN, Maspons J, Sol D. 2018 Predictable evolution towards larger brains in birds colonizing oceanic islands. *Nature Comm.* **9**, 2820. (doi: 10.1038/s41467-018-05280-8)

93. Healy SD, Rowe C. 2007 A critique of comparative studies on brain size. *Proc. R. Soc. - Biol. Sci.* **274**, 453-464. (doi: 10.1098/rspb.2006.3748)

94. Font E, García-Roa R, Pincheira-Donoso D, Carazo P. 2019 Rethinking the effects of body size on the study of brain size evolution. *Brain Behav. Evol.* **93**, 182-195. (doi: 10.1159/000501161)

95. Galea LAM, Kavaliers M, Ossenkopp KP, Innes D, Hargreaves EL. 1994 Sexually dimorphic spatial learning varies seasonally in two populations of deer mice. *Brain Res.* **635**, 18-26. (doi: 10.1016/0006-8993(94)91419-2)

96. Barrett BJ et al. 2018 Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *R. Soc. open Sci.* **5**, 181002. (doi: 10.1101/351619)

97. Rutz C, St Clair JJH. 2012 The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behav. Processes* **89**, 153–165. (doi: 10.1016/j.beproc.2011.11.005)

98. Rutz C et al. 2016 Discovery of species-wide tool use in the Hawaiian crow. *Nature* **537**, 403–407. (doi: 10.1038/nature19103)

99. Tebbich S, Sterelny K, Teschke I. 2010 The tale of the finch: adaptive radiation and behavioural flexibility. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 1099–1109. (doi: 10.1098/rstb.2009.0291)

100. Auersperg AMI, Szabo B, von Bayern AMP, Kacelnik A. 2012 Spontaneous innovation in tool manufacture and use in a Goffin’s cockatoo. *Curr. Biol.* **22**, R903–R904. (doi: 10.1016/j.cub.2012.09.002)

101. Snell-Rood EC. 2013 An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* **85**, 1004-1011. (doi: 10.1016/j.anbehav.2012.12.031)

102. Cabrera, D., Nilsson, J. R., & Griffen, B. D. 2021. The development of animal personality across ontogeny: a cross-species review. *Anim. Behav.* **173**, 137-144. (doi: 10.1016/j.anbehav.2021.01.003)

103. Kotrschal A, Taborsky B 2010 Environmental change enhances cognitive abilities in fish. *PLoS biology* **8**, e1000351. (doi: 10.1371/journal.pbio.1000351)

104. Meuthen D, Ferrari MCO, Lane T, Chivers DP. 2019 Plasticity of boldness: high perceived risk eliminates a relationship between boldness and body size in fathead minnows. *Anim. Behav.* **147**, 25-32. (doi: 10.1016/j.anbehav.2018.11.003)

105. Liedtke, J., Redekop, D., Schneider, J. M., & Schuett, W. 2015 Early environmental conditions shape personality types in a jumping spider. *Front. Ecol. Evol* **3**, 134. (doi: 10.3389/fevo.2015.00134)

106. Hunter DS, Hazel SJ, Kind KL et al. 2016 Programming the brain: Common outcomes and gaps in knowledge from animal studies of IUGR. *Physiol. Behav.* **164**, 233-248. (doi: 10.1016/j.physbeh.2016.06.005)

107. Laus MF, Manhas Ferreira V, Duarte L et al. 2011 Early postnatal protein-calorie malnutrition and cognition: a review of human and animal studies. *Int. J. Environm. Res. Publ. Health* **8**, 590-612. (doi: 10.3390/ijerph8020590)

108. Arnold KE, Ramsay SL, Donaldson C et al. 2007 Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. *Proc. Royal Soc. B-Biol. Sci.* **274**, 2563-2569. (doi: 10.1098/rspb.2007.0687)

109. Blondel J, Aronson J. 1999 *Biology and wildlife of the Mediterranean region.* Oxford, UK: Oxford Univ. Press. (doi: 10.1080/00222933031000156213)

110. Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. 2016 Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* **182**, 55-69. (doi: 10.1007/s00442-016-3648-8)

111. Henke-von der Malsburg J, Kappeler PM, Fichtel C. 2020 Linking ecology and cognition: does ecological specialisation predict cognitive test performance? *Behav. Ecol. Sociobiol.* **74**, 154. (doi: 10.1007/s00265-020-02923-z)

112. Ashton BJ, Thorton A, Ridley AR. 2018 An intraspecific appraisal of the social intelligence hypothesis. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **373**, 20170288. (doi: 10.1098/rstb.2017.0288)

113. Croston, R., Branch, C. L., Kozlovsky, D. Y., Dukas, R., & Pravosudov, V. V. 2015 Heritability and the evolution of cognitive traits. *Behav. Ecol.* **26**, 1447-1459. (doi: 10.1093/beheco/arv088)

114. Mayr E 1942. Systematics and the Origin of Species. Columbia Univ. Press , New York.

115. Raffard A, Cucherousset J, Prunier JG, Loot G, Santoul F, Blanchet S. 2018 Variability of functional traits and their syndromes in a freshwater fish species (*Phoxinus phoxinus*): The role of adaptive and nonadaptive processes. *Ecol. Evol.* **9**, 2833-2846. (doi: 10.1002/ece3.4961)

116. Gruber J, Brown G, Whiting MJ, Shine R. 2018 Behavioural divergence during biological invasions: a study of cane toads (*Rhinella marina*) from contrasting environments in Hawai'i. *R. Open Sci.* **5,** 180197. (doi: 10.1098/rsos.180197)

117. Frankham, R. 1998 Inbreeding and extinction: island populations. *Conservation Biology* **12**, 665-675. (doi: 10.1111/j.1523-1739.1998.96456.x)

118. Charlesworth D. 2003 Effects of inbreeding on the genetic diversity of populations. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **358**, 1051-1070. (doi: I 10.1098/rstb.2003.1296)

119. Charlesworth D, Willis JH. 2009 The genetics of inbreeding depression. *Nature Rev. Gen.* **10**, 783-796. (doi: 10.1038/nrg2664)

120. Herdegen-Radwan M. 2019 Does inbreeding affect personality traits? *Ecol. Evol.* **9**, 10929-10937. (doi: 10.1002/ece3.5487)

121. Verweij KJH, Yang J, Lahti J et al. 2012 Maintenance of genetic variation in human personality: testing evolutionary models by estimating heritability due to common causal variants and investigating the effect of distant inbreeding. *Evolution* **66**, 3238-3251. (doi: 10.1111/j.1558-5646.2012.01679.x)

122. Müller T, Juškauskas A. 2018 Inbreeding affects personality and fitness of a leaf beetle. *Anim. Behav.* **138**, 29-37. (doi: 10.1016/j.anbehav.2018.02.002)

123. Morton NE. 1978 Effect of inbreeding on mental retardation. *Proc. Natl. Acad. Sci. USA* **75**, 3906-3908. (doi: 10.1073/pnas.75.8.3906)

124. Alvarez G, Ceballos FC, Quintero C. 2009 The role of inbreeding in the extinction of a European royal dynasty. *PLoS One* **4**, e5174. (doi: 10.1371/journal.pone.0005174)

125. Howrigan DP, Simonson MA, Davies G, Harris SE, Tenesa A, Starr JM et al. 2016 Genome-wide autozygosity is associated with lower general cognitive ability. *Mol. Psychiatry* **21**, 837-843. (doi: 10.1038/mp.2015.120)

126. Gandin I, Faletra F, Faletra F, Carella M, Pecile V, Ferrero GB, et al. 2015 Excess of runs of homozygosity is associated with severe cognitive impairment in intellectual disability. *Genet. Med.* **17**, 396-399. (doi: 10.1038/gim.2014.118)

127. Joshi PK, Esko T, Mattson H, Eklund N, Gandin I et al. 2015 Directional dominance on stature and cognition in diverse human populations. *Nature* **523**, 459-462. (doi: 10.1038/nature14618)

128. Kornilov SA, Tan M, Aljughaiman A, Naumova OY, Grigorenko EL. 2019 Genome-wide homozygosity mapping reveals genes associated with cognitive ability in children from Saudi Arabia. *Front. Genet.* **10**, 888. (doi: 10.3389/fgene.2019.00888)

129. Nepoux V, Haag CR, Kawecki TJ. 2010 Effects of inbreeding on aversive learning in *Drosophila*. *J. Evol. Biol.* **23**, 2333-2345. (doi: 10.1111/j.1420-9101.2010.02094.x)

130. Harker KT, Whishaw IQ. 2002 Place and matching-to-place spatial learning affected by rat inbreeding (Dark–Agouti, Fischer 344) and albinism (Wistar, Sprague–Dawley) but not domestication (wild rat vs. Long–Evans, Fischer–Norway). *Behav. Brain Res.* **134**, 467-477. (doi: 10.1016/s0166-4328(02)00083-9)

131. Ducrest, A. L., Keller, L., & Roulin, A. 2008 Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol. Evol.* **23**, 502-510. (doi: doi:10.1016/j.tree.2008.06.001)

132. Biro, P. A., & Stamps, J. A. 2008 Are animal personality traits linked to life-history productivity?. *Trends Ecol. Evol.* **23**, 361-368. (doi: 10.1016/j.tree.2008.04.003)

133. Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. 2010 Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **365**, 4051-4063. (doi: 10.1098/rstb.2010.0208)

134. Royauté, R., Hedrick, A., & Dochtermann, N. A. 2020 Behavioural syndromes shape evolutionary trajectories via conserved genetic architecture. *Proc. Royal Soc. B-Biol. Sci.* **287**, 20200183. (doi: 10.1098/rstb.2010.0208)

135. Klomberg KF, Garland TJr, Swallow JG, Carter PA. 2002 Dominance, plasma testosterone levels, and testis size in house mice artificially selected for high activity levels. *Physiol. Behav.* **77**, 27-38. (doi: 10.1016/s0031-9384(02)00767-9)

136. Pelhaitre A, Mignon-Grasteau S, Bertin A. 2012 Selection for wheat digestibility affects emotionality and feeding behaviours in broiler chicks. *Appl. Anim. Behav. Sci.* **139**, 114-122. (doi: 10.1016/j.applanim.2012.03.007)

137. Kolss M, Kawecki TJ. 2012 Reduced learning ability as a consequence of evolutionary adaptation to nutritional stress in *Drosophila melanogaster*. *Ecol. Entomol.* **33**, 583-588. (doi: 10.1111/j.1365-2311.2008.01007.x)

138. Burger JMS, Kolss M, Pont J et al. 2008 Learning ability and longevity: A symmetrical evolutionary trade-off in *Drosophila*. *Evolution* **62**, 1294-1304. (doi: 10.1111/j.1558-5646.2008.00376.x)

139. Sagonas K, Pafilis P, Valakos E 2015. Effects of insularity on digestion: living on islands induces shifts in physiological and morphological traits in island reptiles. Sci. Nat. 102: 1301 (doi: 0.1007/s00114-015-1301-8)

140. Wasser DE , Sherman PW 2010. Avian longevities and their interpretation under evolutionary theories of senescence. *J. Zool.* **280,** 103-155 (doi: 10.1111/j.1469-7998.2009.00671.x)

141. Raia P et al. 2010. The blue lizard spandrel and the island syndrome. *BMC Evol. Biol.* **10,** 289 (doi: 10.1186/1471-2148-10-289)

142. Cody ML, Overton JM. 1996 Short-term evolution of reduced dispersal in island plant populations. *J. Ecol.* **84**, 53-61. (doi: 10.2307/2261699)

143. Freedman MG, Dingle H, Strauss SY et al. 2020 Two centuries of monarch butterfly collections reveal contrasting effects of range expansion and migration loss on wing traits. *Proc. Natl. Acad. Sci. USA* **117**, 28887-28893. (doi: 10.1073/pnas.2001283117)

144. Simberloff, D. and Wilson, E. O. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* **50**, 278–296. (doi:10.2307/1934856)

145. García-Verdugo et al. 2017. The loss of dispersal on islands hypothesis revisited: Implementing phylogeography to investigate evolution of dispersal traits in *Periploca* (Apocynaceae). *J. Biogeogr.* **44,** 2595–2606 (doi: https://doi.org/10.1111/jbi.13050)

146. Burns KC 2019. Time to abandon the loss of dispersal ability hypothesis in island plants: A comment on Garcia-Verdugo, Mairal, Monroy, Sajeva and Caujape-Castells (2017). *J. Biogeogr.* **45,** 1219-122 (doi: 10.1111/jbi.13223)

147. Chapple DG, Simmonds SM, Wong BB 2012 Can behavioral and personality traits influence the success of unintentional species introductions?. *Trends Ecol. Evol.* **27**, 57-64. (doi: 10.1016/j.tree.2011.09.010)

148. Price, T. D., & Sol, D. 2008 Introduction: genetics of colonizing species. *Am. Nat* **172**, S1-S3. (doi: : 10.1086/588639)

149. Foster BJ et al. 2021. Anthropogenic evolution in an insect wing polymorphism following widespread deforestation. Biol. Lett. **17**, 20210069 (doi:2021006920210069)

150. McCullogh GA et al. 2021. Genomic signatures of parallel alpine adaptation in recently evolved flightless insects. *Molec. Ecol.* **30**, 6677-6686. (doi: 10.1111/mec.16204)

151. Donald D 1985. The wing length of *Sweltsa revelstoka* (Plecoptera, Chloroperlidae). *Can. Entomol.* **117,** 233-239.

152. Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010 Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Phil. Trans. R. Soc. B* **365**, 4065-4076. (doi: 10.1098/rstb.2010.0176)

153. Wey TW, Spiegel O, Montiglio PO, Mabry KE. 2015 Natal dispersal in a social landscape: Considering individual behavioral phenotypes and social environment in dispersal ecology. *Curr. Zool.* **61**, 543-556. (doi: 10.1093/czoolo/61.3.543)

154. Schradin C, Lamprecht J. 2002 Causes of female emigration in the group-living cichlid fish *Neolamprologus multifasciatus*. *Ethology* **108**, 237-248. (doi: 10.1046/j.1439-0310.2002.00775.x)

155. Qu J, Chen Q, Zhang Y. 2017 Behaviour and reproductive fitness of postdispersal in plateau pikas (*Ochotona curzoniae*) on the Tibetan Plateau. *Mammal Res.* **63**, 151-159. (doi: 10.1007/s13364-017-0344-y)

156. Trefilov A, Berard J, Krawczak M, Schmidtke J. 2000 Natal dispersal in rhesus macaques is related to serotonin transporter gene promoter variation. *Behav. Genet.* **30**, 295-301. (doi: 10.1023/a:1026597300525)

157. Michelangeli M, Smith CR, Wong BBM, Chapple DG. 2017 Aggression mediates dispersal tendency in an invasive lizard. *Anim. Behav.* **133**, 29-34. (doi: 10.1016/j.anbehav.2017.08.027)

158. Hoset KS, Ferchaud AL, Dufour F, Mersch D, Cote J, Le Galliard JF. 2011 Natal dispersal correlates with behavioral traits that are not consistent across early life stages. *Behav. Ecol.* **22**, 176-183. (doi: 10.1093/beheco/arq188)

159. Blumstein DT, Wey TW, Tang K. 2009 A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc. Royal Soc. B-Biol. Sci.* **276**, 3007-3012. (doi: 10.1098/rspb.2009.0703)

160. Cote J, Clobert J. 2007 Social personalities influence natal dispersal in a lizard. *Proc. Royal Soc. B-Biol. Sci.* **274**, 383-390. (doi: 10.1098/rspb.2006.3734)

161. Liedtke J, Fromhage L. 2021 The joint evolution of learning and dispersal maintains intraspecific diversity in metapopulations. *Oikos* **130**, 808-818. (doi: 10.1111/oik.08208)

162. Maille A, Schradin C. 2016 Survival is linked with reaction time and spatial memory in African striped mice. *Biol. Lett.* **12**, 20160346. (doi: 10.1098/rsbl.2016.0346)

163. Vincze O. 2016 Light enough to travel or wise enough to stay? Brain size evolution and migratory behavior in birds. *Evol.* **70**, 2123-2133. (doi: doi.org/10.1111/evo.13012)

164. Szabo B, Damas-Moreira I, Whiting MJ. 2020 Can cognitive ability give invasive species the means to succeed? A review of the evidence. *Front. Ecol. Evol.* **8**, 187. (doi: 10.3389/fevo.2020.00187)

165. Dingemanse NJ, Both C, Drent PJ, Tinbergen JM. 2004 Fitness consequences of avian personalities in a fluctuating environment. *Proc. Royal Soc. B-Biol. Sci.* **271**, 847-852. (doi: 10.1098/rspb.2004.2680)

166. Bell AM, Sih A. 2007 Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol. Letters* **10**, 828-834. (doi: 10.1111/j.1461-0248.2007.01081.x)

167. Garamszegi LZ, Zagalska-Neubauer M, Canal D, Marko G, Szasz E et al. 2015 Malaria parasites, immune challenge, MHC variability, and predator avoidance in a passerine bird. *Behav. Ecol.* **26**, 1292-1302. (doi: 10.1093/beheco/arv077)

168. Keiser CN, Ingley SJ, Toscano BJ, Scharf I, Pruitt JN. 2018 Habitat complexity dampens selection on prey activity level. *Ethology* **124**, 25-32. (doi: 10.1111/eth.12700)

169. Schuett W, Tregenza T, Dall SRX. 2010 Sexual selection and animal personality. *Biol. Rev.* **85**, 217-246. (doi: 10.1111/j.1469-185x.2009.00101.x)

170. Munson, A. A., Jones, C., Schraft, H., & Sih, A. 2020 You’re just my type: mate choice and behavioral types. *Trends Ecol. Evol.* **35**, 823-833. (doi: 10.1016/j.tree.2020.04.010)

171. Anaya-Meraz, Z. A., & Escobedo-Galván, A. H. 2020 Insular effect on sexual size dimorphism in the clouded anole *Anolis nebulosus*: when Rensch meets Van Valen. *Curr. Zool.* **66**, 589-591. (doi: 10.1093/cz/zoaa034)

172. Roulin, A. & Salamin, N. 2010 Insularity and the evolution of melanism, sexual dichromatism and body size in the worldwide-distributed barn owl. *J. Evol. Biol.* 23, 925–934. (doi: 10.1111/j.1420-9101.2010.01961.x)

173. Moiron, M., Laskowski, K. L., & Niemelä, P. T. 2020 Individual differences in behaviour explain variation in survival: A meta-analysis. *Ecol. Lett.* **23**, 399-408. (doi: 10.1111/ele.13438)

174. Humphrey N. 1976 The social function of intellect. In Growing points in ethology (eds Bateson PPG, Hinde RA), pp. 303-317, Cambridge, UK: Cambridge University Press. (doi: 10.1016/0003-3472(77)90136-1)

175. Ashton BJ, Kennedy P, Radford AN. 2020 Interactions with conspecific outsiders as drivers of cognitive evolution. Nat. Commun. **11**, 1–9. (doi: 10.1038/s41467-020-18780-3)

176. Parker ST, Gibson KR. 1977 Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in *Cebus* monkeys and great apes. *J. Hum. Evol.* **6,** 623-641. (doi: 10.1016/s0047-2484(77)80135-8)

177. Sol D. 2009 Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biol. Lett.* **5**, 130-133. (doi: 10.1098/rsbl.2008.0621)

178. Allman JM. 2000 *Evolving brains*. New York, NY: Scientific American Library, Freeman and Company New York.

179. Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199-221. (doi: 10.1086/204350)

180. van Horik J, Emery NJ. 2011 Evolution of cognition. *Wiley Interdiscip. Rev. Cogn. Sci.* **2**, 621-633. (doi: 10.1002/wcs.144)

181. McGowen MR, Grossman LI, Wildman DE. 2012 Dolphin genome provides evidence for adaptive evolution of nervous system genes and a molecular rate slowdown. *Proc. Royal Soc. B-Biol. Sci.* **279**, 3643-3651. (doi: 10.1098/rspb.2012.0869)

182. Miller SE, Legan AW, Henshaw MT, Ostevik KL, Samuk K, et al. 2020 Evolutionary dynamics of recent selection on cognitive abilities. *Proc. Natl. Acad. Sci. USA* **117**, 3045-3052. (doi: 10.1073/pnas.1918592117)

183. Orkin JD, Montague MD, Tejada-Martinez D, de Manuel M, del Campo J, et al. 2021 The genomics of ecological flexibility, large brains, and long lives in capuchin monkeys revealed with fecalFACS. *Proc. Acad. Natl. Sci.* **118**, e2010632118. (doi: 10.1101/366112)

184. Evans PD, Gilbert SL, Mekel-Bobrov N, Vallender EJ, Anderson JR, Vaez-Azizi LM et al. 2005 Microcephalin, a gene regulating brain size, continues to evolve adaptively in humans. *Science* **309**, 1717-1720. (doi: 10.1126/science.1113722)

185. Agrillo C, Bisazza A 2018. Understanding the origin of number sense: a review of fish studies. *Phil. Trans. R. Soc. B* **373,** 20160511 (doi: /10.1098/rstb.2016.0511)

186. Shettleworth SJ 2009) The evolution of comparative cognition: is the snark still a boojum? *Behav. Processes* **80,** 210-217 (doi: 10.1016/j.beproc.2008.09.001).

187. De Meester G, Baeckens S 2021. Reinstating reptiles: from clueless creatures to esteemed models of cognitive biology. *Behaviour* **158,** 1057-1076 (doi: 10.1163/1568539X-00003718)

188. Perry CJ, Barron AB, Chittka L 2017. The frontiers of insect cognition. *Curr. Opinion Behav. Sci.* **16,** 111–118 (doi: 10.1016/j.cobeha.2017.05.011)

189. Mitchell DJ, Beckmann C, Biro PA. 2020 Predation as a driver of behavioural variation and trait integration: effects on personality, plasticity, and predictability. *EcoEvoRxiv.* August 17. (doi:10.32942/osf.io/jwd3c)

190. Brown C, Braithwaite VA 2005. Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. *Behav. Ecol.* **16**, 482-487. (doi: 10.1093/beheco/ari016)

191. Jaatinen K, Møller A, Öst M. 2019 Annual variation in predation risk is related to the direction of selection for brain size in the wild. *Sci. Rep.* **9**, 11847. (doi: 10.1038/s41598-019-48153-w)

192. Mortelliti A, Brehm AM. 2020 Environmental heterogeneity and population density affect the functional diversity of personality traits in small mammal populations. *Proc. R. Soc. – Ser. Biol*. **287**,20201713. (doi: 10.1098/rspb.2020.1713)

193. Wolf M, Weissing FJ 2010. An explanatory framework for adaptive personality differences. *Phil. Trans. R. Soc. B – Biol. Sci.* **365**, 3959-3968. (doi: 10.1098/rstb.2010.0215)

194. Poirier, M. A., Kozlovsky, D. Y., Morand-Ferron, J., & Careau, V. (2020). How general is cognitive ability in non-human animals? A meta-analytical and multi-level reanalysis approach. *Proc. R. Soc. B.* **287**, 20201853. (doi: 10.1098/rspb.2020.1853)

195. Liedtke J, Fromhage L 2019. Modelling the evolution of cognitive styles. *BMC Evol. Biol.* **19,** 234. (doi: 10.1186/s12862-019-1565-2)

196. Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. 2007 Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**, 581-584. (doi: 10.1038/nature05835)

197. Careau V, Garland T Jr 2012 Performance, personality, and energetics: correlation, causation, and mechanism. Physiol. Biochem. Zool. 85: 543-571. (doi: 10.1086/666970)

198. Roulin A, Ducrest AL 2010 Association between melanism, physiology and behaviour: A role for the melanocortin system. *Eur. J. Pharmacol.* **660**, 226-233. (doi: 10.1016/j.ejphar.2011.01.036)

199. Goulet CT, Michelangeli M, Chung M et al. 2018 Evaluating cognition and thermal physiology as components of the pace-of-life syndrome. *Evol. Ecol.* **32**, 469-488. (doi: 10.1007/s10682-018-9948-1)

200. Arnold S.J., Pfrender M.E., Jones A.G. 2001 The adaptive landscape as a conceptual bridge between micro- and macroevolution. In: Hendry A.P., Kinnison M.T. (eds) *Microevolution Rate, Pattern, Process. Contemporary Issues in Genetics and Evolution*, vol 8. Springer, Dordrecht. (doi: 10.1007/978-94-010-0585-2_2)

201. Arnold, S. J., Bürger, R., Hohenlohe, P. A., Ajie, B. C., & Jones, A. G. 2008 Understanding the evolution and stability of the G-matrix. *Evolution* **62**, 2451-2461. (doi: 10.1111/j.1558-5646.2008.00472.x)

202. Schluter, D. (1996). Adaptive radiation along genetic lines of least resistance. *Evolution* **50**, 1766-1774. (doi: 10.1111/j.1558-5646.1996.tb03563.x)

203. Freedman MG, Dingle H, Strauss SY et al. 2020 Two centuries of monarch butterfly collections reveal contrasting effects of range expansion and migration loss on wing traits. *Proc. Natl. Acad. Sci. USA* **117**, 28887-28893. (doi: 10.1073/pnas.2001283117)

204. Sih, A., & Del Giudice, M. 2012 Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Phil. Trans. R. Soc. B – Biol. Sci.* **367**, 2762-2772. (doi: 10.1098/rstb.2012.0216)

205. McWaters SR, Pangle WM. 2021 Heads up! Variation in the vigilance of foraging chipmunks in response to experimental manipulation of perceived risk. *Ethology* **127**, 309-320. (doi: 10.1111/eth.13128)

206. Blumstein DT, Daniel JC, Springett BP. 2004 A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* **110**, 919–934. (doi: 10.1111/j.1439-0310.2004.01033.x)

207. Humphrey PS, Livezey BC, Siegel-Causey D. 1987 Tameness of birds of the Falkland Islands: An index and preliminary results. Bird Behav. 7, 67-72. (doi: 10.3727/015613887791918114)

208. Rasheed AA, Hambley K, Chan G, de la Rosa CA, Larison B, Blumstein DT. 2017 Persistence of antipredator behavior in an island population of California quail. Ethology 124, 155-160. (doi: 10.1111/eth.12716)

209. Rödl T, Berger S, Romero LM, Wikelski M. 2007 Tameness and stress physiology in a predator-naive island species confronted with novel predation threat. Proc. Royal Soc. B-Biol. Sci. 274, 577-582. (doi: 10.1098/rspb.2006.3755)

210. Blázquez MC, Rodríguez-Estrella R, Delibes M 1997. Escape behavior and predation risk of mainland and island spiny-tailed iguanas (Ctenosaura hemilopha). Ethology 103: 990-998. (doi: 10.1111/j.1439-0310.1997.tb00141.x)

211. Stone PA, Snell HL, Snell HM. 1994 Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. Conserv. Biol. 8, 569-573. (doi: 10.1046/j.1523-1739.1994.08020569.x)

212. Cooper WE Jr, Pérez-Mellado V. 2012 Historical influence of predation pressure on escape by Podarcis lizards in the Balearic Islands. Biol. J. Linn. Soc. 107, 254-268. (doi: 10.1111/j.1095-8312.2012.01933.x)

213. Cooper WE Jr, Hawlena D, Pérez-Mellado V. 2009 Islet tameness: escape behavior and refuge use in populations of the Balearic lizard (Podarcis lilfordi) exposed to differing predation pressure. Can. J. Zool. 87, 912-919. (doi: 10.1139/z09-077)

214. Vervust B, Grbac I, Van Damme R. 2007 Differences in morphology, performance and behaviour between recently diverged populations of Podarcis sicula mirror differences in predation pressure. Oikos 116, 1343-1352. (doi: 10.1111/j.0030-1299.2007.15989.x)

215. Cooper WE Jr, Pyron RA, Garland T Jr. 2014 Island tameness: living on islands reduces flight initiation distance. Proc. Royal Soc. B-Biol. Sci. 281, 20133019. (doi: 10.1098/rspb.2013.3019)

216. Li BB, Belasen A, Pafilis P, Bednekoff P, Foufopoulos J. 2014 Effects of feral cats on the evolution of anti-predator behaviours in island reptiles: insights from an ancient introduction. Proc. Royal Soc. B-Biol. Sci. 281, 20140339. (doi: 10.1098/rspb.2014.0339)

217. Brock KM, Bednekoff PA, Pafilis P, Foufopoulos J. 2015 Evolution of antipredator behavior in an island lizard species, Podarcis erhardii (Reptilia: Lacertidae): The sum of all fears? PeerJ 8, e10284. (doi: 10.1111/evo.12555)

218. De Meester G, Lambreghts Y, Briesen B, Smeuninx T, Tadić Z, Van Damme R. 2018 Hunt or hide: How insularity and urbanization affect foraging decisions in lizards. Ethology 124, 227-235. (doi: 10.1111/eth.12722)

219. Välimäki K, Hinten G, Hanski I. 2007 Inbreeding and competitive ability in the common shrew (*Sorex araneus*). *Behav. Ecol. Sociobiol.* **61**, 997-1005. (doi: 10.1007/s00265-006-0332-8)

220. Kubo D, Kono RT. 2011 Endocranial restoration and volume estimation of the Minatogawa IV cranium using micro-CT and 3D printer systems. *Anthropol. Sci.* **119**, 201-209. (doi: 10.1537/ase.110228)

221. Diniz-Filho JAF, Raia P. 2017 Island rule, quantitative genetics and brain–body size evolution in *Homo floresiensis*. *Proc. Royal Soc. B-Biol. Sci.* **284,** 20171065. (doi: 10.1098/rspb.2017.1065)

222. Masters JC, Genin F, Silvestro D, Lister AM, DelPero M. 2014 The red island and the seven dwarfs: body size reduction in Cheirogaleidae. *J. Biogeogr.* **41**, 1833-1847. (doi: 10.1111/jbi.12327)

223. Köhler M, Moya-Soya S. 2004 Reduction of brain and sense organs in the fossil insular bovid Myotragus. Brain Behav. Evol. 63, 125-140. (doi: 10.1159/000076239)

224. Quintana J, Köhler M, Moya-Sola S. 2011 Nuralagus rex, gen. et sp. nov., an endemic insular giant rabbit from the Neogene of Minorca (Balearic Islands, Spain). J. Vertebr. Paleontol. 31, 231-240. (doi: 10.1080/02724634.2011.550367)

225. Duhamel A, Hume JP, Guenser P, Salaviale C, Louchart A. 2020 Cranial evolution in the extinct Rodrigues Island owl Otus murivorus (Strigidae), associated with unexpected ecological adaptations. Sci. Rep. 10, 14019. (doi: 10.1038/s41598-020-69868-1)

226. Scofield RP, Ashwell KWS. 2020 Rapid somatic expansion causes the brain to lag behind: the case of the brain and behavior of New Zealand's Haast's eagle (Harpagornis moorei). J. Vertebr. Paleontol. 29, 637-649. (doi: 10.1671/039.029.0325)

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]).

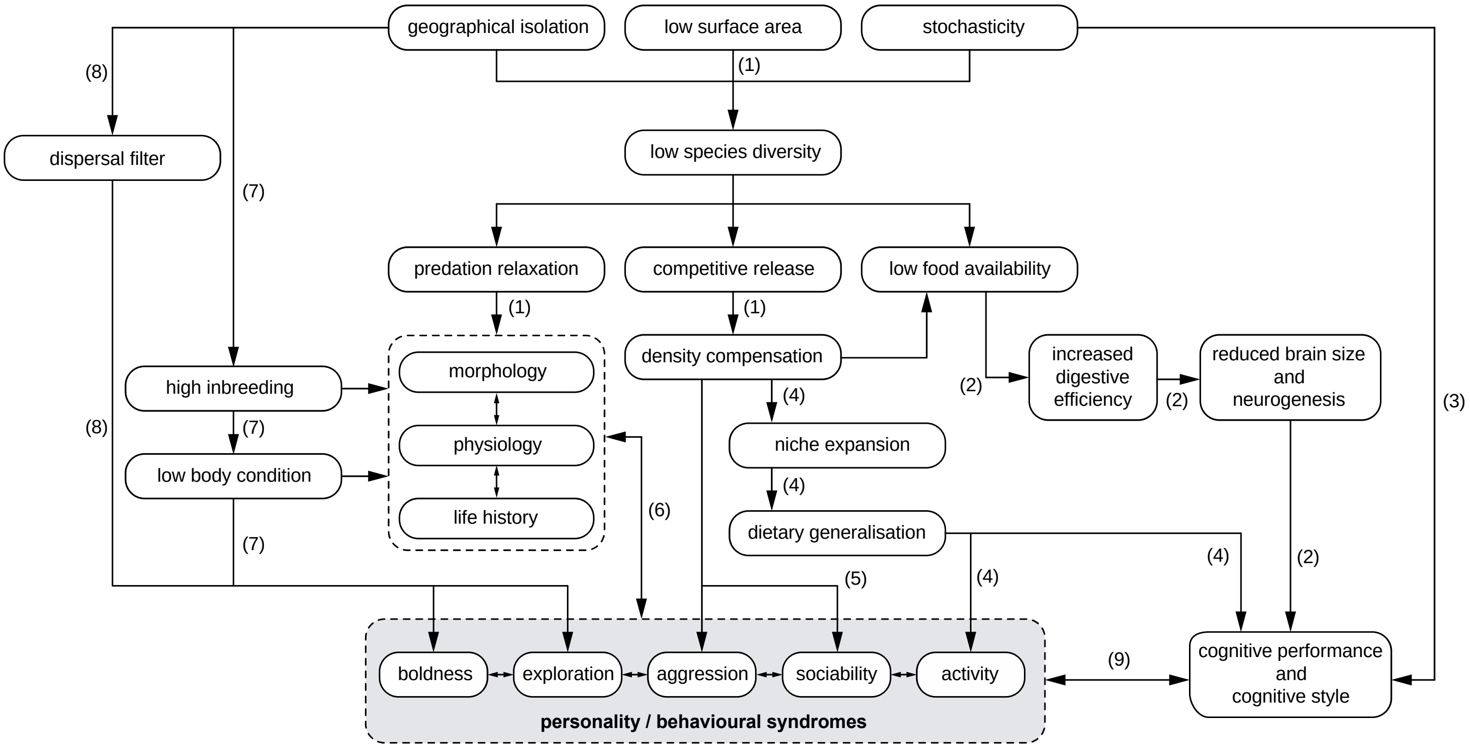

Table 1: — Studies that have compared behavioural, personality or cognitive (including brain morphology studies) traits between island and mainland, or among island populations/species. The ‘driver’ and ‘mechanism’ are those suggested (but not necessarily demonstrated) by the authors. FID stands for Flight Initiation Distance. The ‘type of analysis’ also indicates whether the study includes repeated within-individual measurements (personality variation).

Study species	Trait	Island	Mainland	Driver	Mechanism	Type of analysis	Reference
Personality							
Eastern chipmunks (*Tamias striatus*)	Island chipmunks are less vigilant, but both island and mainland specimens adjust vigilance to microhabitat structure	Beaver Island, Michigan, USA	two sites on mainland Michigan	lower predation pressure on island (checked with camera traps)	unknown	field experiments; personality variation measured	[205]
14 species of macropodid marsupials	animals on islands are less wary and allocate more time to foraging; no effect on FID	Satellite islands of Australia	Australia	predation pressure	acknowledges possibilities of plasticity and selection	field observations; comparative analysis	[206]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Reindeer (*Rangifer tarandus*)	island reindeer are more vigilant on the island, but response distances are the same	Edgeoya, Norway	4 sites on Spitsbergen, Norway	possibly higher predation (by polar bears) on island	response distance believed to be 'hard-wired'	field observations	[40]
Bull-headed shrike (*Lanius bucephalus*)	Longer FID in island shrikes	Kikaijima, Minami-daitojima and Nakanoshima Islands, Japan	3 sites on main Japanse Islands	risk of predation (by rats) higher on islands	genetic change, plasticity and dispersal-related selection are considered	field observations	[41]
11 species of Falkland island birds	FID is lower on island than on mainland	Falkland Islands	mainland Argentina	absence of terrestrial predators	probably innate, evolutionarily acquired, but habituation also deemed possible	field observations; comparative analysis	[207]
California quail (*Callipepla californica*)	FID is similar on mainland and island, but SD* is smaller on islands	Santa Catalina Island, USA	California, USA	some predators lacking on island	assumed genetic ('antipredator genes')	field observations	[208]

Study species	Trait	Island	Mainland	Driver	Mechanism	Type of analysis	Reference
Orange-throated whiptail (*Aspidoscelis hyperythra*)	island lizards are more difficult to catch than mainland lizards	7 Gulf of California islands	Baja California	predation pressure, human collection for pet trade	reasoned to be genetically based, implying rapid evolution of antipredator behaviour	field observations	[42]
Galápagos marine iguanas (*Amblyrhynchus cristatus*)	lizards on predator-free islet have shorter FIDs; although FID increases with experience, it remains insufficient to avoid predation	Caamaño Islet, Galápagos, Ecuador	St Cruz and San Cristobal Island, Galápagos, Ecuador	predation pressure	release from predation narrowed the reaction norm for FID	field observations	[209]
Spiny-tailed iguanas (*Ctenosaura hemilopha*)	island lizards behave less wary and have shorter FIDs than mainland lizards	Cerralvo Island, Gulf of California	Mexico	low predation pressure on the island	no hints	field observations	[210]
Lava lizards (8 populations of three *Tropidurus* spp.)	lizards on islands with introduced cats have higher FID	8 islands of the Galapagos	no mainland population	presence of exotic predators (cats)	could be inherited, or learned	field observations; comparative analysis	[211]

Study species	Trait	Island	Mainland	Driver	Mechanism	Type of analysis	Reference
Ibiza wall lizards (*Podarcis pityusensis*)	FID and distance fled is greater on islets with higher predation pressure	7 islets around Ibiza and Formentera, Spain	no mainland population	predation pressure as estimated by number and kind of predators, incl. humans	unknown, both phenotypic plasticity and evolutionary processes deemed possible	field observations; comparative analysis	[212]
Lilford's wall lizard (*Podarcis lilfordi*)	FID, distance fled, hiding time and probability to enter refuge are lower on islet with less predators	Islets of Rei and Aire (Menorca, Spain)	no mainland population	predation pressure	natural selection	Field observations	[213]
Italian wall lizard (*Podarcis siculus*)	FID is shorter on island with lower predation pressure	comparison between two islands in the Adriatic Sea	no mainland population	predation pressure, through number of predators and habitat structure	unknown	field observations	[214]
66 lizard species	FID decreases as distance to mainland increases	islands in the Atlantic and Pacific Oceans; Caribbean and Mediterranean Seas	5 continents	predation pressure is lower on islands; reduced food availability may shorten FID to save energy	probably genetic changes, but tameness might be learned every generation	field observations; comparative analysis	[215]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Aegean wall lizard (*Podarcis erhardii*)	lizards from islets have shorter FID and act bolder than lizards from main island	4 satellite islands of Naxos, Greece	18 populations on Naxos, Greece	cat predation	phenotypic plasticity; which is also maintained on islets	field observations; lab experiments	[216]
38 populations of Aegean wall lizards (*Podarcis erhardii*)	lizards from smaller and more isolated islets have shorter FIDs	37 Cycladic islands	mainland Greece	predation	natural selection	field observations	[217]
Lilford's wall lizard (*Podarcis lilfordi*)	FID and distance fled is not correlated with predation pressure	9 islets around Menorca and Mallorca, Spain	no mainland population	predation pressure as estimated by number and kind of predators, incl. humans	unknown, both phenotypic plasticity and evolutionary processes deemed possible	field observations; comparative analysis	[212]
Dalmatian wall lizard (*Podarcis melisellensis*)	islet lizards are bolder, less wary but not less neophobic than island lizards	3 small islets out of the coast of Vis, Croatia	Vis, Croatia	food availability, predation pressure smaller on islets	selection, plasticity or non-random gene-flow are suggested	field experiments	[218]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Common frog (*Rana temporaria*)	enhanced boldness and exploration in island tadpoles and froglets	4 islands in the Gulf of Bothnia, Sweden	Sweden	dispersal propensity; unstable conditions on islands (pond drying); reduced predation on islands	founder effects caused by environmental filtering or differential natural selection	lab experiments with wild-caught specimen; personality variation and behavioural syndrome measured	[57]
House mice (*Mus musculus domesticus*)	enhanced boldness and exploration on island	Gough Island	Maryland, US	novel food source (sea birds), loss of predatory danger, removal of human commensals, variable food availability	genetic change	common garden experiment with F1-offspring	[56]
61 species of parrots (Psittacidae)	Island species explore novel objects faster and longer than mainland species; island species are not less neophobic than mainland species.	several, not specified	several sites, not specified	reduced predation pressure and higher risk of food shortage on islands	assumed genetic	comparative analysis; behavioural syndrome across species tested, but not at the individual level, or between island and mainland species	[59]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Island scrub jays (*Aphelocoma insularis*) vs California scrub jay (*A. californica*)	island birds were more explorative than mainland birds	Santa Cruz Island, California, USA	mainland California, USA	reduced predation, more frequent food shortage on island	unknown	field observations/experiments	[60]
Brown anoles (*Anolis sagrei*)	lizards on islands with introduced predators are less explorative	8 small islands in the Caribbean, on four of which predatory lizards were introduced	no mainland population	presence of introduced predators (lizards)	natural selection	fitness gradient analysis; personality variation measured	[58]
Red-backed vole (*Myodes gapperi*)	island voles are less aggressive than mainland voles; no difference in exploration	10 islands in the Winnipeg River, Ontario, Canada	6 sites on mainland Ontario	relaxed predation, higher population density	dispersal-related, ecological and evolutionary mechanisms all considered	lab experiment; comparative analysis	[62]
Deer mice (*Peromyscus maniculatus*)	wild-caught island mice are less aggressive, but difference disappears in subsequent generations	Saturna Island, Pender Island	British Columbia, Canada	population density thought to reduce aggressiveness	phenotypic plasticity	lab experiment with wild-caught specimen and their offspring; crossings	[67]

Study species	Trait	Island	Mainland	Driver	Mechanism	Type of analysis	Reference
Deer mice (*Peromyscus maniculatus*)	island mice do not show aggressive behaviour towards juveniles; some mainland mice behave aggressively towards non-kin.	Saturna Island, Canada	British Columbia, Canada	reduced intraspecific competition due to high food supply on island	Unknown	lab test on P (interact with F1)	[68]
Common shrew (*Sorex araneus*)	island and mainland shrews equally aggressive	4 islands in the Baltic Sea	2 sites on mainland Finland	island specimens often inbred		lab experiments with field-caught individuals	[219]
Skyros wall lizard (*Podarcis gaigeae*)	islet lizards more likely to attack juveniles and behave more aggressively to other adults	islet Diavates	Skyros main island	food scarcity and high population size prompt for cannibalism	Unknown	lab experiments with field-caught individuals	[75]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Tiger snakes (*Notechis scutatus*)	adult snakes from predator-rich sites have more vigorous responses when handled, but neonatal behaviour is unrelated to predator species richness	8 islands around Australia	3 sites, on mainland Australia and Tasmania	predation pressure, through number and type of predators	ontogenetic plasticity; experience, or genetically coded adjustment of behaviour to ontogenetically variable traits	observations on freshly caught individuals	[71,72]
Common garter snakes (*Thamnophis sirtalis*)	adult but not neonate snakes from the mainland behave more aggressively towards experimentor than island snakes	Beaver Archipelago, USA	Michigan, USA	fewer predators on island	both innate and environmental influences	laboratory behavioural observations	[73]
Pacific rattlesnake (*Crotalus oreganus*)	island snakes behave more aggressively towards humans	Santa Catalina Island, USA	mainland California, USA	island has fewer avian predators but perhaps more (introduced) mammalian predators	Unknown	field observations	[74]

Study species	Trait	Island	Mainland	Driver	Mechanism	Type of analysis	Reference
Chuckwalla species (*Sauromalus* spp.)	island endemics are more sociable, less aggressive than mainland species	San Esteban Island and Angel Island, California, USA	mainland California, USA	dearth of predators, competitors, niche expansion, high but fluctuating food supply, high density on island	Unknown	field observations	[77]
House mice (*Mus musculus domesticus*)	island mice do not show aggressive, defensive or cautious behaviour towards conspecifics	Isle of May, UK	Nottinghamshire, UK	interaction between resource distribution, habitat structure and predation risk	Unknown	lab experiments on recently caught specimens	[69]
Yellow-faced grass-quit (*Tiaris olivacea*)	island birds are more territorial than mainland birds, which occur more often in flocks	Jamaica	Costa Rica	island density is lower	Unknown	field observations	[78]

Study species	Trait	Island	Mainland	Driver	Mechanism	Type of analysis	Reference
Human (*Homo sapiens*)	islanders exhibit greater animosity towards strangers and keep greater social distance	Croatian Islands	mainland Croatia	dangers associated with infectious disease		Questionnaire	[81]
Human (Homo sapiens)	islanders had higher levels of consciousness, emotional stability and lower levels of extraversion and opennes; no difference in agreeableness	Giglio, Ponza and Ventotene, and seven Aeolian islands, Italy	3 sites on mainland Italy	island is harsh, restricted environment with limited social environment	assumed adaptive (changes in same direction); elimination of well less adapted through mortality, assortative mating or emigration	Questionnaire	[63-65]
Meadow voles (*Microtus pennsylvanicus*) versus beach voles (*M. breweri*)	island species is more sociable	Muskeget Island, Massachusetts, USA	mainland Massachusetts, USA		differential dispersal of intolerant specimens	field observations	[76]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
46 species of birds	birds on islands tend to flock less than birds on the mainland	22 different islands	22 mainland sites to match islands	predation pressure	random drift or active selection are suggested	comparative analysis	[79]
Long-tailed macaques (*Macaca fascularis*)	smaller group sizes on island	Simeulue, Indonesia	Sumatra, Indonesia	felid predation	unknown	field observations	[80]
Tammar wallabies (*Macropus eugenii*)	time allocation is dependent on group size on mainland and islands with reduced number of predators, but not on predator-free island	Garden Island, Kangaroo Island, Australia; Kawau Island, New Zealand	Western Australia	absence of predators	maintained by natural selection, but 'priming agents' may be required to develop antipredator behaviour	field observations	[206]
Oriental fire-bellied toads (*Bombina orientalis*)	island toads have lower levels of activity	Jeju Island, South Korea	2 sites on mainland South Korea	predation is higher on island	local selection, founder effects also considered possible	lab observations	[83]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Clouded anoles (*Anolis nebulosus*)	island anoles are more active	San Agustín, México	mainland México	less variable environmental conditions on island may allow better thermoregulation; higher predation on mainland		field observations	[82]
Cognition							
Minatogawa man (*Homo sapiens*) versus modern Japanese and Pleistocene/Holocene *H. sapiens*.	Pleistocene island dwellers had relatively small endocrania	Okinawa Island, Japan	mainland Japan	undernutrition	phenotypic plasticity; genetic adaptation	comparative analysis of brain size	[220]
Human (*Homo floresiensis* versus *Homo erectus*)	relative brain size is lower in island species	Flores, Indonesia		biotic interactions and resource use	natural selection for smaller brains (in addition to selection for smaller body size).	quantitative genetic modelling	[221]
Mouse and dwarf lemurs (Cheirogaleidae)	disproportional reduction in brain size in this island clade	Madagascar		unpredictable food availability	natural selection	comparative analysis of brain size	[222]

Study species	Trait	Island	Mainland	Driver	Mechanism	Type of analysis	Reference
Malagasy dwarf hippos (*Hippopotamus lemerle*i, *H. madagascariensis*) versus hippopotamus (*H. amphibius*)	relative brain size is lower in island species	Madagascar	mainland Africa	poor dietary resources on islands	natural selection for smaller brains (in addition to selection for smaller body size).	ontogenetic modelling	[85]
Siculo-Maltese dwarf elephant (*Palaeoloxodon falconer*i) versus P. antiquus	relative brain size is lower in island species	Malta	mainland Africa	poor dietary resources on islands	natural selection for smaller brains (in addition to selection for smaller body size).	ontogenetic modelling	[85]
Siculo-Maltese dwarf elephant (*Palaeoloxodon falconer*i) versus P. antiquus	dwarfed insular species has a high encephalization quotient	Sicily, Italy	mainland Europe		need to maintain the minimal functional volume of the brain when the size of the skull was drastically reduced	allometric analysis	[86]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Balearic Islands cave goat (*Myotragus* spp.) compared to 54 spp. of extant bovids	insular species have small brain and sense organs relative to body size	Balearic Islands, Spain	mainland Africa	absence of predators; overpopulation; limited energy availability	natural selection for smaller brains (in addition to selection for smaller body size).	scaling analysis	[223]
Cretan deer (*Candiacervus*), compared to extant deer (Cervidae)	insular dwarf deer have normal relative brain size	Crete, Greece		dearth of predators on islands		comparative analysis of brain size	[87]
Sardinian dhole (*Cynotherium sardous*), compared to 2 spp of extant dog spp. (Canidae)	insular dwarf canid has normal relative brain size	Sardinia, Italy				comparative analysis of brain size	[88]
Minorcan giant rabbit (*Nuralagus rex*), compared to extant rabbit species (Leporidae)	Late neogene insular giant had relatively small brain; especially sense-dependent areas are small	Minorca, Balearic Islands, Spain		absence of predators; limited energy availability		comparative analysis of brain size	[224]
426 mammalian species	no effect of insularity on relative brain size	islands worldwide	mainland sites throughout the world	poor dietary resources on islands	natural selection for smaller brains	comparative analysis of brain size	[90]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
Dodo (*Raphus cucullatus*) compared to 9 spp of pigeons (Columbiformes)	endocranial volume not smaller than expected from pigeon-allometry	Mauritius				allometric analysis	[89]
Rodrigues Island giant owl *(Otus murivorus), compared to 10 extant spp. Owls (Strigidae)*	reduction of brain volume in extinct island endemic	Rodrigues, Mauritius	diverse	absence of predators, reduction of interspecific competition	brain expansion cannot follow pace of body size increase ('evolutionary pace dissociation')	comparative analysis of brain size	[225]
Haast's eagle (*Harpagornis moorei*), compared to 35 spp of eagles (Accipitridae)	island endemic had low endocranial volume for its body mass	New Zealand	diverse	absence of predators, competitors on island	mismatch between neural and somatic growth	comparative analysis of brain size	[226]
40 Crow and raven species (*Corvus*)	brain size does not predict ability to colonize islands	islands worldwide	mainland sites throughout the world	islands are challenging environments, promoting enhanced cognition		comparative analysis of brain size	[91]

Study species	**Trait**	**Island**	**Mainland**	**Driver**	**Mechanism**	**Type of analysis**	**Reference**
>1900 species of birds	insular species have larger brains	diverse	diverse	high environmental unpredictability across years	natural selection; high phenotypic plasticity may inhibit evolutionary change in some clades	comparative analysis of brain size	[92]

Table 2: — Outstanding questions on the evolution of personality and cognition on islands

THE MASTER DATA
Do island populations exhibit repeatable inter-individual differences in the way they behaviourally interact with their environment, and are these differences consistent across contexts? 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? Do animal populations on islands differ in cognitive skills from their counterparts on the mainland, or on other islands?
THE MECHANISMS OF CHANGE
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? 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? What is the role of phenotypic plasticity versus genetic adaptation in creating differences in cognition and personality between island and mainland populations?
THE DRIVERS OF CHANGE
What is the effect of predator release on islands on personality traits? Are these effects general, or specific to a predatory context? 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?

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?