

1 The evolutionary ecology of nest construction: insight
2 from recent fish studies

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19 Running head: *Nest building in fish and birds*

20 **Abstract**

21 Nests are built by a wide variety of animals as functional receptacles for developing
22 eggs and offspring, and they play a critical role in the reproductive biology of many
23 species. Traditionally, research on the ecology and evolution of nesting building and
24 construction behaviour has focused primarily on birds, and avian studies have
25 dominated the literature. However, as researchers working on non-bird models have
26 realised the importance of nest construction in evolutionary ecology, the number of
27 studies published on the nesting behaviour of non-bird taxa has increased. An analysis
28 of the literature reveals that fish have become major models for studying many
29 aspects of nest building behaviour, but whereas studies of fish nest building behaviour
30 frequently cite classical and contemporary bird studies, the findings of recent fish
31 nesting research appears to be slower to be recognised by bird biologists. Further
32 analysis reveals that this citation bias may arise because of the tendency of nest
33 building studies to be published in taxon-specific, often local journals, and this may
34 be especially the case for bird-focused studies. In this review I summarise the recent
35 literature on fish nesting behaviour, focusing on aspects that should be of mutual
36 interest to fish and bird biologists. I hope that the review may be used by bird
37 biologists to identify complimentary and insightful nest-building research in fish, and
38 that researchers with interests in the nest-building behaviour of animals across the
39 taxonomic spectrum might use the review to focus on questions of mutual and general
40 importance and interest.

41 **1. Introduction: nest building in fish and birds**

42 Animals across a broad taxonomic spectrum construct nests that serve as functional
43 receptacles for their eggs and developing offspring (Hansell, 2005, 2007). Given the
44 critical importance of nests in determining the survival of offspring, it is expected that
45 nest building behaviour should be under strong natural selection, and that nest design,
46 construction and structure should be adapted by processes of natural selection to local
47 environmental conditions. Hence we expect that variation in nest construction
48 behaviour within and between species should relate to differences in the ecology and
49 environments occupied by individuals and populations. Moreover, it is increasingly
50 recognised that because some aspects of nest construction and/or design may play an
51 important role in mate choice, nest building may also be subject to processes of sexual
52 selection. For these reasons and others, the nest construction behaviour of animals has
53 therefore become recognised by a wide variety of lab- and field-based biologists –
54 including those with interests in animal cognition, physiology, behaviour, ecology and
55 evolutionary processes – as a topic demanding detailed academic investigation. The
56 study of nest building is facilitated because nests are often visible, collectable and
57 measurable, because nest-building behaviours may be readily quantified, and because
58 museums often house large collections of nests that are available for study. The
59 construction behaviour of animals also has intrinsic public interest (e.g. Hansell *et al.*,
60 2000), giving opportunities for the participation of ‘citizen scientists’ and the
61 dissemination of results through the popular as well as the scientific media.

62 Evolutionary, ecological and environmental aspects of nest building are studied in a
63 wide variety of animals, from invertebrates to primates (Fig. 1a). In the fields of
64 evolutionary and behavioural ecology, birds have proved exceptional models for the
65 study of nesting behaviour, and avian studies dominate the literature; however, over

66 recent years there has been an increase in the number of research groups studying the
67 nest building behaviour of fish, and a concomitant increase in the number of fish
68 nesting publications (Fig. 1b).

69

70 *1.1 Nest building fishes: who and how?*

71 Nest construction is a taxonomically dispersed behaviour in teleost fishes, and the
72 types of behaviour exhibited and the emergent structures that are built vary
73 considerably (Reebs, 2001). Nesting behaviour in fish ranges from the elementary –
74 such as the cleaning of rock surfaces prior to the deposition of eggs by some cichlid
75 species, or the digging of simple depressions ('redds') in gravel spawning substrate by
76 female salmonids – to the sophisticated, with some fish species exhibiting meticulous
77 material selection, construction behaviour and, in some cases, the use of specialised
78 endogenous substances in construction. Despite the widespread taxonomic
79 distribution of nest building in teleosts, the majority of contemporary nest building
80 studies have focused on a relatively small number of species, including members of
81 the Gasterosteidae (sticklebacks) and the Gobiidae (gobies). In particular, the three-
82 spined stickleback *Gasterosteus aculeatus*, which is common across the northern
83 hemisphere in all aquatic habitat types in marine, brackish and freshwater
84 environments (Wootton, 1976), and for which there is a fully sequenced and
85 increasingly well-annotated genome (Jones *et al.*, 2012), has emerged as the pre-
86 eminent fish model for use in evolutionary ecology studies (Barber and Nettleship,
87 2010). Consequently, many of the studies covered in this review involve these
88 species, though examples from other species are included whenever possible.

89

90 *1.2 Barriers to the transfer of knowledge across taxonomic boundaries*

91 Often the types of questions addressed by biologists using fish and bird models differ,
92 and in some cases this reflects the different backgrounds and research fields
93 traditionally associated with the two taxonomic groups. For example, many classical
94 bird studies used a cognitive psychological framework to investigate the role of
95 learning and experience in the nest construction of birds (Collias and Collias, 1964,
96 Sargent, 1965, Collias and Collias, 1973), and this approach has been developed
97 successfully in the modern era (e.g. Muth and Healy, 2011, Walsh *et al.*, 2011). In
98 contrast, to the author's knowledge no fish studies have addressed cognitive aspects
99 of nest building, though a recent increase in studies examining the role of fish
100 cognition in other behaviours (Brown and Laland, 2003, Coolen *et al.*, 2003, Pike and
101 Laland, 2010, Webster and Laland, 2011) suggests such an approach may be possible.

102 However, in many cases despite differences in the biology of the organisms
103 themselves, or in the challenges presented by constructing nests in terrestrial and
104 aquatic environments, the questions being asked by researchers examining nest
105 building behaviour in fish and birds are converging. Given this convergence on
106 question of broad general interest, we should be expect that research findings from
107 across the taxonomic spectrum should be being utilised. However, the results of nest
108 building studies are reported in journals representing a wide range of academic sub-
109 disciplines (see Fig. 2 and Appendix), and almost half of the papers published over
110 the last 50 years or so have been published in taxon-specific journals that may not
111 always be widely available to, or regularly accessed by, all researchers. When coupled
112 with the fact that results are also discussed at taxonomically themed meetings, there is
113 potential to generate parallel fields of research, with rather less crossover of

114 knowledge than might be expected, given the ready availability of web-based
115 bibliographic searching tools.

116

117 *1.3 Aims of the review*

118 My aim in this short review is to summarise some of the major recent findings of
119 studies examining aspects of the evolutionary ecology of nest building in fish, and to
120 relate these to studies addressing similar questions in birds. I will focus primarily on
121 three major topics of mutual interest to fish and bird researchers: ecological
122 adaptation and plasticity in nest construction, the role of sexual selection in nest
123 design and the effects of anthropogenic impacts on nest building behaviour. In doing
124 so, I hope to identify similarities and differences in the questions being addressed, in
125 the approaches being taken and the results being generated, and to stimulate interest in
126 the possibility of making greater gains in knowledge through collaborative studies.

127

128 **2. Ecological adaptation and plasticity in nest construction**

129 A major field of interest in both bird and fish nesting research is the study of
130 ecological adaptation and plasticity in nest building behaviour and nest design.
131 Aquatic and terrestrial environments differ in a wide range of physical properties,
132 which place divergent pressures on the construction and design of nests. Although
133 fish and bird nests may perform equivalent functions and, in some cases, appear
134 similar in form, it is important to recognise that the methods of construction, the
135 materials that are used and the factors affecting their construction can vary
136 considerably.

137

138 *2.1 Adaptation of nests to thermal regimes*

139 As endotherms, birds – and particularly small temperate passerines – expend a
140 significant amount of energy in thermoregulation (Bartholm and Trost, 1970, Dawson
141 *et al.*, 1983, Nagy, 1987). Developing embryos and chicks are especially sensitive to
142 both overheating and cooling (Webb, 1987) and can be exposed to rapid fluctuations
143 in temperature as a result of diurnal and longer-term seasonal climatic changes. A
144 primary function of bird nests is therefore to protect their contents from extremes of
145 temperature (Hilton *et al.*, 2004, Asokan *et al.*, 2008, Heenan and Seymour, 2012).
146 Bird nests may also need to provide eggs and chicks with protection from
147 precipitation – which can generate evaporative cooling effects – and cooling
148 convection currents (Heenan and Seymour, 2012). A number of studies have
149 demonstrated that birds are capable of adjusting the thermal qualities of nests in
150 response to fluctuating environmental temperatures to maintain optimal nest
151 microclimates. Both long tailed tits *Aegithalos caudatus* and blue tits *Cyanistes*
152 *caeruleus* vary the mass of feathers incorporated into nests as ambient temperatures to
153 ensure consistent thermal environment (McGowan *et al.*, 2004, Mainwaring and
154 Hartley, 2008). Recent investigations have also revealed that the mass of lining
155 material incorporated into blue tit nests varies systematically along latitudinal clines
156 in the UK, suggesting adaptive divergence in populations (Mainwaring *et al.*, 2012).
157 By contrast, the physical properties of water means that aquatic environments provide
158 a more buffered, thermally stable medium for nest building, at least over the typical
159 lifetime of an active fish nest. Hence, thermoregulation is not an important factor
160 influencing nest design in fish, although – because the speed of embryo development

161 in fish is closely tied to ambient water temperatures (Pepin, 1991) – spatial variation
162 in temperature associated with water depth, shading or local water currents may
163 influence nest site choice. Thermal regimes may also play an indirect role in nest
164 construction in fish because dissolved oxygen (dO₂) levels, which impact nesting
165 behaviour and nest structure substantially (see 3.2 below), correlate closely and
166 negatively with water temperature.

167

168 *2.2 Dissolved oxygen*

169 The bioavailability of oxygen is a far more important factor influencing the design
170 and construction of fish nests than temperature *per se*. Although reduced oxygen
171 levels may cause problems for offspring development in some cavity nesting birds
172 such as woodpeckers (Ar *et al.*, 2004), it is unlikely to pose a major limitation on
173 design for most bird nests. In contrast, dissolved oxygen (dO₂) levels can vary
174 substantially both temporally and spatially in aquatic ecosystems, and the
175 development of fish embryos is frequently oxygen-limited (Malcolm *et al.*, 2010).
176 Laying eggs into an enclosed nest that limits water movements means that in most
177 cases nest building or cavity nesting fish species need to engage in fanning behaviour
178 to waft oxygenated water over developing eggs, and this can constitute an
179 energetically demanding and costly element of parental care (Jones and Reynolds,
180 1999a, Lissaker *et al.*, 2003). There is also evidence that nest site choices, nest design
181 and construction behaviour have evolved to mitigate the typically low and variable
182 bioavailability of oxygen in aquatic environments. For example, bluegill sunfish
183 *Lepomis macrochirus* inhabiting ponds with spatially variable dO₂ levels choose well-
184 oxygenated sites at which to build nests (Gosch *et al.*, 2006).

185 Members of the sand goby group (*Pomatoschistus* spp.) are small marine fish that
186 occupy shallow water habitats and typically build nests by excavating substrate from
187 underneath empty bivalve shells and depositing it on top. Under conditions of low
188 dO₂, male sand gobies *Pomatoschistus minutus* construct nests that have larger
189 entrance holes than when under favourable dO₂ conditions, where males keep nest
190 holes small to counter the threat of predation (Jones and Reynolds, 1999c, b, Lissaker
191 *et al.*, 2003) or sexual competition from other males (Svensson and Kvarnemo, 2003).
192 Three spined sticklebacks alter the structure of nests through the nesting cycle; as
193 embryos develop and have higher energetic demands, sticklebacks successively
194 reduce the compactness of their nests (Wunder, 1930), presumably to enhance the
195 availability of dO₂.

196

197 *2.3 Coping with dynamic shearing forces*

198 Both aquatic and terrestrial environments are subject to dynamic shearing forces
199 generated by water and air currents, so both fish and birds may be required to select
200 sheltered sites, robustly anchor nests, or otherwise construct nests that are resistant to
201 these forces. Birds often fasten nests securely by weaving or knotting the nest material
202 to supporting structures, and this is facilitated by precise control afforded by the use
203 of the beak, which allows the fine manipulation required in such behaviour (Hansell,
204 2000). Although some fish, such as nine-spined sticklebacks *Pungitius pungitius*, are
205 capable of performing simple weaving or ‘looping’ behaviour to attach their nests to
206 submerged vegetation (Morris, 1958, Zyuganov, 1986), fish nests are more commonly
207 placed in crevices or beneath rocks, or anchored to the substratum by the deposition
208 of material (e.g. sand, fine gravel) on top. Some birds and fish use endogenous

209 secretions that act as glues and play an important role in anchoring nests. Some cliff-
210 nesting birds use such secretions to mix with nesting material to increase the
211 adhesiveness and / or structural rigidity of nests; this is perhaps exemplified most
212 extremely in Chinese swiftlets (genus *Collocalia*) which use mucus glycoproteins,
213 produced in the salivary gland, as a nest cementing substance that hardens in air
214 (Wieruszeski *et al.*, 1987). Sticklebacks secrete endogenous mucous-like glue –
215 named ‘spiggin’, after the Swedish for stickleback ‘*Spigg*’ (Jakobsson *et al.*, 1999) –
216 which facilitates the sticking together of nesting materials underwater. This glue is
217 produced in copious amounts in the kidney of sexually mature males and is coded for
218 by a family of genes that are closely related to vertebrate mucin genes (Jones *et al.*,
219 2001).

220 Fish can exhibit behavioural plasticity in nest construction in response to changes in
221 flow regimes. In an experimental study, designed to investigate the effects of
222 increased water flow rates on nest structure, individual male three spined sticklebacks
223 built smaller and more elongate nests – and incorporated more Spiggin per gram of
224 nest – than when building under no-flow conditions (Rushbrook *et al.*, 2010).
225 Similarly, under increasing water flow rates, male river blennies adjust the position of
226 nest entrance holes such that at the highest flow rates they face 180° to the direction of
227 flow (Vinyoles *et al.*, 2002). Subtle adjustment of nest orientation in this species
228 ensures that the rate of water flow reaching the nest entrance remains remarkably
229 consistent, between 5-7cm.sec⁻¹, despite highly variable flow rates. A remarkably
230 similar behaviour is observed among lesser skylarks (*Alauda gulgula wattersi*), which
231 typically orient nest openings at 180° to the direction of prevailing winds (Yuan,
232 1996). Many other birds also select nest sites that are sheltered from prevailing winds
233 and wind-driven precipitation; water pipits (*Anthus spinoletta*) in alpine tundra build

234 nests that are sunken into depressions (Boehm and Landmann, 1995) and in the
235 Algerian Sahara, Houbara bustards (*Chlamydotis undulata undulate*) build nests under
236 tufts of vegetation to provide shelter from northern winds (Gaucher, 1995).

237 The selection of nesting materials may also be selected to counter the risks of washout
238 from water currents. Both three- and nine-spined sticklebacks invest considerable
239 time in testing the buoyancy of nest materials prior to their incorporation into nests
240 (Morris, 1958, Wootton, 1976). Hornyhead chubb (*Nocomis biguttatus*) are cyprinid
241 fish that construct large dome-shaped nests of gravel and pebbles in fast flowing
242 riverine environments, which are often used secondarily as spawning substrates for
243 other smaller species (Miller *et al.*, 2005). Gravel mounds are typically built in areas
244 with relatively high, though less than maximum available, flow rates. However,
245 pebbles selected for constructing the nest are of smaller diameter and higher density
246 than non-utilised pebbles, maximising the resistance of nests to washout during spates
247 (Wisenden *et al.*, 2009).

248

249 *2.4 The influence of predators and parasites*

250 Both terrestrial bird nests and those built by fishes underwater are subject to
251 exploitation by a wide range of predators and parasitic organisms, though the nature
252 of these threats varies both between and within nesting taxa. Predators impose
253 particularly strong selection on nest site choices, nest construction behaviour and nest
254 design in birds (Lima, 2009). For example, the concealment of eggs with nest material
255 shown by mallards *Anas platyrhynchos* has been demonstrated to significantly reduce
256 the risk of nest predation (Kreisinger and Albrecht, 2008) and the choice of pebble
257 colouration in the simple nests of piping plovers also plays a role in camouflaging the

258 clutch (Mayer *et al.*, 2009). Siberian jays *Perisoreus infaustus* show significant
259 changes in nest site preferences after artificial manipulation of perceived predation
260 threat via playback of predator calls, selecting increasingly protected nest sites
261 (Eggers *et al.*, 2006). In an almost directly analogous study in sticklebacks, the
262 presence of egg predators induces preferences for structurally complex nest sites (i.e.
263 in vegetation) over generally preferred open sites (Candolin and Voigt, 1998).

264 Nestling birds are attacked by a wide variety of ectoparasitic arthropods (Moreno *et*
265 *al.*, 2009), and are also under threat from bacterial infections (Singleton and Harper,
266 1998, Berger *et al.*, 2003). Eggs too are susceptible to attack by microbes, and
267 strategic distribution of antimicrobial proteins to eggs (Shawkey *et al.*, 2008, D'Alba
268 *et al.*, 2010b) and the drying of eggs during incubation can both serve to reduce levels
269 of infection (D'Alba *et al.*, 2010a). There is increasing evidence that some birds
270 actively incorporate green plant materials with biocidal properties into their nests
271 (Mennerat *et al.*, 2009), and in some cases this behaviour may improve chick survival
272 and performance (Gwinner *et al.*, 2000). In fish, the egg stage is most vulnerable to
273 infection, most often by bacteria and microparasitic fungi, including the ubiquitous
274 aquatic oomycete *Saprolegnia parasitica*. Although there is no evidence that fish
275 select nesting materials to reduce losses to parasitic infections, the nesting glue of
276 sticklebacks has been demonstrated to have antibacterial properties, and the eggs from
277 glue-containing nests have a higher probability of hatching (Little *et al.*, 2008).

278

279 **3. Nests as ornaments in fish and birds**

280 Nests primarily serve as functional receptacles for developing eggs and offspring, and
281 so it is not surprising that females often exhibit preferences to lay eggs in nests that

282 are ‘fit for purpose’. Accordingly, female penduline tits *Remiz pendulinus* show
283 preferences for larger better insulated nests (Hoi *et al.*, 1996), and benefit by doing so
284 because they can invest less time in incubating the eggs (Grubbauer and Hoi, 1996).
285 Similarly, female red bishops *Euplectes orix* preferred male-built nests that were
286 woven more densely and had more overlapping entrance roofs, traits related to nest
287 durability (Metz *et al.*, 2009).

288 However, nests and other artefacts may also be viewed as classical examples of extra-
289 organismal ‘extended phenotypes’, defined as traits that arise from the expression of
290 an organism’s genes but that have direct effects on environments (Dawkins, 1982).
291 There is considerable interest in the idea that such extended phenotypic traits might
292 act as extra-bodily signals of individual quality, which may be used by mate searching
293 individuals as honest indicators of quality (Schaedelin and Taborsky, 2009). In birds,
294 a number of studies have correlated attributes of nest structure with male phenotypic
295 traits, including immune function (De Neve *et al.*, 2004, Soler *et al.*, 2007),
296 suggesting that female preferences for nests may not relate solely to their functional
297 capacity as receptacles for eggs or offspring, but also because they provide reliable
298 indicators of male quality (Evans, 1997, Jose Sanz and Garcia-Navas, 2011).

299 In the simplest case, nest size in fish can indicate body size, as in the corkwing wrasse
300 *Symphodus melops* (Uglem and Rosenqvist, 2002). Barber *et al.* (2001) provided
301 some of the first data that the structure of male-built nests might convey other useful
302 information to female fish, since male three-spined sticklebacks with greater levels of
303 kidney hypertrophy – indicative of circulating androgen levels – built nests that were
304 neater and more compact. In sticklebacks, the kidney is the site of nesting glue
305 (‘Spiggin’) biosynthesis (Jakobsson *et al.*, 1999), so one explanation is that males
306 with larger kidneys build higher quality nests at least partly because they have an

307 abundance of glue to stick together nesting materials. In an experimental study of
308 marine fifteen-spined sticklebacks *Spinachia spinachia*, the number of glue threads
309 secreted into nests was related to feeding ration; males fed higher rations incorporated
310 more threads, suggesting that nest composition may reflect energetic status, which in
311 turn might indicate their parental ability. Further, when choosing among males that
312 had been fed similar rations, female fifteen-spined sticklebacks preferred to lay eggs
313 in nests containing more threads, suggesting that females use cues from the nest to
314 make spawning decisions (Östlund-Nilsson, 2001). Evidence that variation in male
315 nest building behaviour might give information to females about male quality also
316 comes from studies examining the effect of debilitating parasite infections. Among
317 sticklebacks infected with the parasitic cestode *Schistocephalus solidus* – which
318 depletes host energy reserves and reduces circulating androgen levels (Barber *et al.*,
319 2008, Macnab *et al.*, 2011) – nest building is most severely affected amongst males
320 harbouring the largest worms (Rushbrook and Barber, 2006, Rushbrook *et al.*, 2007,
321 Macnab *et al.*, 2009). By basing their choice of mates on attributes of the nests they
322 construct, females may therefore avoid the most heavily parasitized, or otherwise
323 energetically challenged males.

324 In *Pomatoschistus* spp. gobies, the amount of sand deposited on top of the nest is
325 uncorrelated with male body size (Svensson and Kvarnemo, 2005), but it is condition-
326 dependent, and so may honestly signal male quality. In experimental studies, male
327 common gobies *P. microps* held in tanks without access to prey were less likely to
328 construct nests (Jackson *et al.*, 2002), and male sand gobies fed on higher rations built
329 bigger nests (Olsson *et al.*, 2009). Female gobies typically show preferences for nests
330 with more deposited sand (Svensson and Kvarnemo, 2005, Lehtonen and Lindstrom,
331 2009, but see Lehtonen and Wong, 2009), which may give protection against

332 predators (Lindstrom and Ranta, 1992). When given a choice between males that
333 differed in body size and nest size, females showed the strongest preference largest
334 nests as long as they were built by large males, suggesting that females use nest size
335 as one of a number of multiple cues in this species (Lehtonen *et al.*, 2007).

336 Some fish construct elaborate ‘bowers’ – display arenas that have no nest function –
337 that appear to fulfil an identical role to those constructed more famously by birds (e.g.
338 Borgia, 1985). In Lake Malawi, a number of genera of cichlids construct volcano-
339 shaped sand bowers, and there is substantial evidence that physical aspects of bowers
340 are repeatable, reflect the quality of individual builders (Schaedelin and Taborsky,
341 2006, Martin and Genner, 2009) and are used by females to choose males (Kellogg *et*
342 *al.*, 2000, Genner *et al.*, 2008, Young *et al.*, 2010). Although there is some
343 controversy over the use of the term ‘bower’ to describe these artefacts, since these
344 cichlids are mouth-brooders that do not construct a separate nest (Tweddle *et al.*,
345 1998), the important point is that the design of the display arena is essentially
346 unrelated to by any nesting function. The existence of artefacts created purely for
347 display purposes by fish therefore raises the possibility that some attributes of
348 functional nests may also serve a purely ornamental purpose. Sticklebacks, for
349 example, are known to incorporate non-structural decorations into their nests, with
350 impacts on mate choice. Östlund-Nilsson & Holmlund (2003) demonstrated that male
351 marine three-spined sticklebacks used ornamental threads, provided at low frequency
352 by the experimenters, to decorate their nests and that females subsequently preferred
353 nests that incorporated these decorations. Furthermore, the artificial addition of
354 brightly coloured threads to three-spined stickleback nests located in the field
355 increased both the level of a male’s courtship and his investment in nest building, and
356 in the lab led to males building neater and more compact nests (Morrell *et al.*, 2012).

357 These results suggest that the energy saved by having an artificially enhanced nest can
358 be reinvested in other aspects of courtship.

359

360 **4. Nest building responses to human-induced rapid environmental change**

361 Understanding the extent to which animals are able to alter their behaviours to cope
362 with human induced rapid environmental change (HIREC), and determining the
363 fitness consequences of such behaviour changes, has become a key topic in
364 evolutionary ecology (Sih *et al.*, 2011, Candolin and Wong, 2012). The impact of
365 HIREC is increasingly a focus of nest building research, in both birds and fish. In
366 birds, nesting responses to introduced predators can be affected. On the Hawaiian
367 island of Oahu, the height at which a forest-dwelling monarch flycatcher (*Chasiempis*
368 *ibidis*) built their nests increased from 7.9m to 12m between 1996 and 2011
369 (Vanderwerf, 2012). The fact that this population level change was not reflected by
370 the behaviour of individuals – which did not change their nest height over successive
371 breeding seasons – suggests a rapid evolutionary rather than a learned response to
372 predation threat. In other cases individual plasticity in behaviour can ‘rescue’ certain
373 species in the face of acute environmental changes; however, not all behavioural
374 changes are likely to be adaptive. ‘Ecological traps’ arise where normally adaptive
375 responses lead to maladaptive outcome in anthropogenically altered environments
376 (Schlaepfer *et al.*, 2002). In birds, there are a number of documented cases of species
377 making poor nest site choices in altered environments. For example, Northern
378 cardinals (*Cardinalis cardinalis*) nesting in exotic shrubs including honeysuckle
379 *Lonicera* sp., incurred significantly higher losses to predators than those nesting in

380 native shrubbery, as a likely result of sub-optimal plant architecture and leaf
381 phenology (Rodewald *et al.*, 2010).

382 Degradation of aquatic ecosystems can result from physical habitat destruction,
383 altered environmental temperatures (as a result of global warming and /or direct input
384 of effluents from industrial cooling processes), altered flow regimes and species
385 introductions. Furthermore, aquatic ecosystems act as sinks for nutrients from
386 agricultural runoff and a wide variety of anthropogenic chemicals, including those
387 with endocrine disrupting actions that affect fish sexual maturation and reproductive
388 behaviours, including nest construction (van der Sluijs *et al.*, 2011). There is
389 increasing interest in the effect of changing environments on fish reproductive
390 behaviour, including nesting behaviour, and a growing body of work examining the
391 impacts of eutrophication (Candolin, 2009). In sticklebacks, increased algal growth
392 creates both greater availability of nesting material and increased numbers of nesting
393 opportunities for sticklebacks (Candolin, 2004, Candolin and Salesto, 2006), meaning
394 that even poor quality individuals in the population may be able to build nests
395 (Heuschele and Candolin, 2010). In such environments, variation in the numbers of
396 eggs acquired by nest-holding males is lower than in non-eutrophic areas, suggesting
397 that females may be less discriminating in their mate choice (Candolin, 2004).

398 Increased opportunities for nesting may therefore reduce overall levels of selection in
399 human impacted habitats. An important side effect of eutrophication, as vegetation
400 begins to decay, is the depletion of dO₂, with knock-on consequences for nesting
401 behaviour (see 3.2 above).

402 Because of their solubility in water, anthropogenic chemicals often impact aquatic
403 organisms more immediately than birds, and there is considerable interest on the
404 effects of chemicals that have endocrine disrupting action in the reproductive biology

405 of fish (Jobling *et al.*, 1998). Nest building behaviour in fish is highly sensitive to
406 such pollutants, with a wide variety of chemicals – including the natural human
407 estrogen 17 β estradiol, synthetic estrogens used in the contraceptive pill, plasticisers
408 such di-N-butyl phthalate and anti-androgenic cancer drugs such as flutamide – all
409 having significant effects on the nest building behaviour of sticklebacks or gobies
410 (Wibe *et al.*, 2002, Sebire *et al.*, 2008, Saaristo *et al.*, 2010, Aoki *et al.*, 2011, Sebire
411 *et al.*, 2011). The reproductive behaviour and physiology, including nest construction
412 and the production of the nesting glue Spiggin, is now widely used as a bioassay for
413 quantifying the sub-lethal effects of anthropogenic chemicals in aquatic environments
414 (Sebire *et al.*, 2008, OECD, 2011).

415

416 **5. Future research directions: are we interested in birds, fish or questions?**

417 It is clear that there is significant overlap in the questions being addressed by
418 researchers investigating nest construction in birds and fish, and that many of these
419 questions – particularly regarding the fitness consequences of behavioural responses
420 to changing environments – require urgent attention. In addressing questions of such
421 general importance, it is imperative that the results of research being undertaken
422 across the taxonomic spectrum are fully utilised. Unfortunately, in the case of nest
423 building behaviour, there is only limited evidence that such taxonomic boundaries to
424 knowledge are being broken down (Fig. 3). An analysis of literature cited in recently
425 published studies on the nesting behaviour of fish and birds, covering topics of broad
426 general interest, reveals that there is limited reference to non-focus taxa, and it seems
427 that the crossing-over of knowledge from fish and bird studies may be asymmetrical,
428 with fish-focused papers more likely to cite bird literature than *vice versa* (Fig. 4).

429 Birds and fish both provide excellent models for the scientific study of nest building;
430 however, they are unlikely to be equally well suited for addressing all questions.
431 Because of their terrestrial nesting habits, the possibility for tracking the survival and
432 reproductive success of offspring in natural field conditions, and the existence of
433 long-term study sites, birds are likely to prove better models for studying the fitness
434 consequences of variation in nest construction or nest structure. In contrast, the many
435 difficulties of studying the reproductive success of fish under natural conditions
436 impose a significant constraint on their use for such studies. Conversely, the small
437 number of offspring produced by birds in a single season largely prohibits the use of
438 quantitative genetic techniques that might otherwise be used to partition the variance
439 in nest construction attributable to genetic and environmental factors. Such techniques
440 are extremely data-hungry and require the production of large numbers of known-
441 pedigree, closely-related offspring (Wilson *et al.*, 2010), and they can be used
442 successfully to identify genetic effects on behaviour in fish (Dingemanse *et al.*, 2009,
443 Dingemanse *et al.*, 2012) and specifically to examine genetic effects on nest building
444 behaviour in turtles (McGaugh *et al.*, 2010). Although the repeatability of nest
445 building behaviour can be studied in fish and birds that build successive nests
446 (Rushbrook *et al.*, 2008, Walsh *et al.*, 2010, Japoshvili *et al.*, 2012), future studies that
447 seek to identify the genetic basis of variation in nest building behaviour are likely to
448 be most successfully undertaken in fish models.

449 Almost all bird species construct nests, so they provide an excellent model for
450 undertaking both large-scale phylogenetic studies of nest construction behaviour
451 (Collias, 1997) and finer scale studies to examine interrelationship between species
452 (Collias and Collias, 1972, Zyskowski and Prum, 1999, Kirwan *et al.*, 2010). Such
453 studies are greatly facilitated by the availability of bird nest collections in museums.

454 Nest building is more sparsely distributed across teleost fishes, however, and
455 phylogenetic approaches have been limited to examining the evolution of nest
456 building *per se* (Hanel *et al.*, 2002, Mank *et al.*, 2005), rather than the types of
457 construction behaviour that have evolved, or of using nest architecture as a means of
458 informing relationships between species.

459 One final reason for developing fish as models for examining questions of general
460 interest in nest building behaviour is related to the welfare concerns surrounding the
461 use of higher vertebrates in scientific research. The 3Rs principles of reduction,
462 refinement and replacement in the use of animals in scientific research (Russell and
463 Burch, 1959) are increasingly advocated, and guidance issued by NC3Rs and similar
464 organisations stipulates that research questions should be addressed “*using species*
465 *that are most likely to produce satisfactory results with the least degree of harm to the*
466 *animals involved*” (Anon, 2008). Most contemporary research on nest building
467 behaviour can be carried out with minimal harm or stress to subjects, and modern
468 field and experimental behavioural scientists strive to implement the highest standards
469 of ethical treatment of study animals. However, where there is a requirement to
470 examine the effects of environmental stressors on nesting behaviour, or to carry out
471 invasive or terminal procedures to better understand – for example – the neurological
472 control of nesting behaviour (Sager *et al.*, 2010), researchers should seek to identify
473 the lowest useful taxonomic group for study. Although there continues to be
474 significant discussion over the consciousness or otherwise of fishes, and their ability
475 to suffer and/or perceive pain (Rose, 2002, Sneddon *et al.*, 2003, Huntingford *et al.*,
476 2006, Braithwaite, 2010), ‘lower’ vertebrates – including fish – might ultimately
477 prove to be more suitable model systems than ‘higher’ vertebrates such as birds for
478 examining basic questions about nest building behaviour under laboratory conditions.

479

480 In conclusion, although biologists investigating the nesting behaviour of birds and fish
481 may often do so to inform the ecology or biology of a particular species – for example
482 with a view to improving its conservation status – it is increasingly the case that
483 studies are undertaken to test more general hypotheses that are of interest and
484 importance across taxonomic boundaries. There is, however, only limited evidence
485 that major findings of studies on fish nesting behaviour are informing contemporary
486 bird studies, and *vice versa*. I hope that this short review may therefore be used as a
487 jumping-off point for bird biologists who may be interested in learning more about
488 the nesting behaviour of fish, and that it may stimulate fish biologists to find out more
489 about contemporary nest building research in birds and other taxa.

490

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FIGURES

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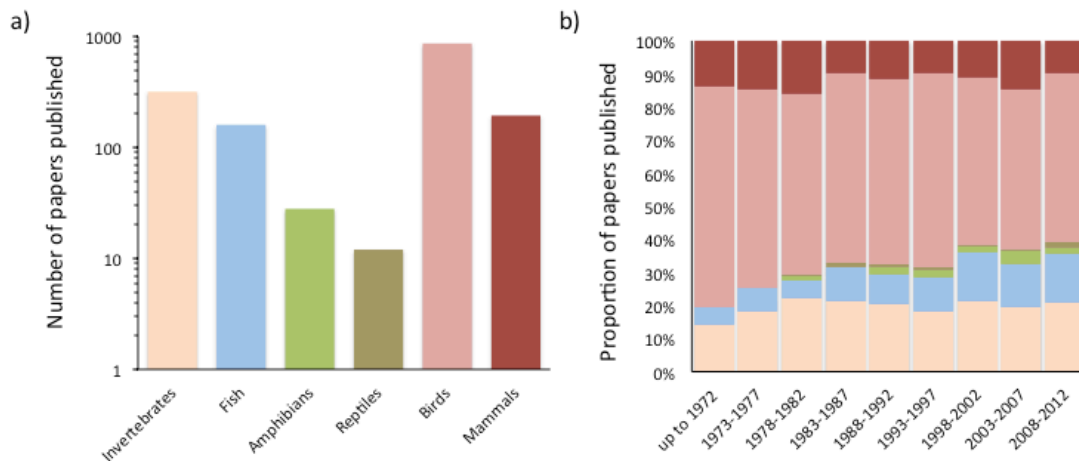
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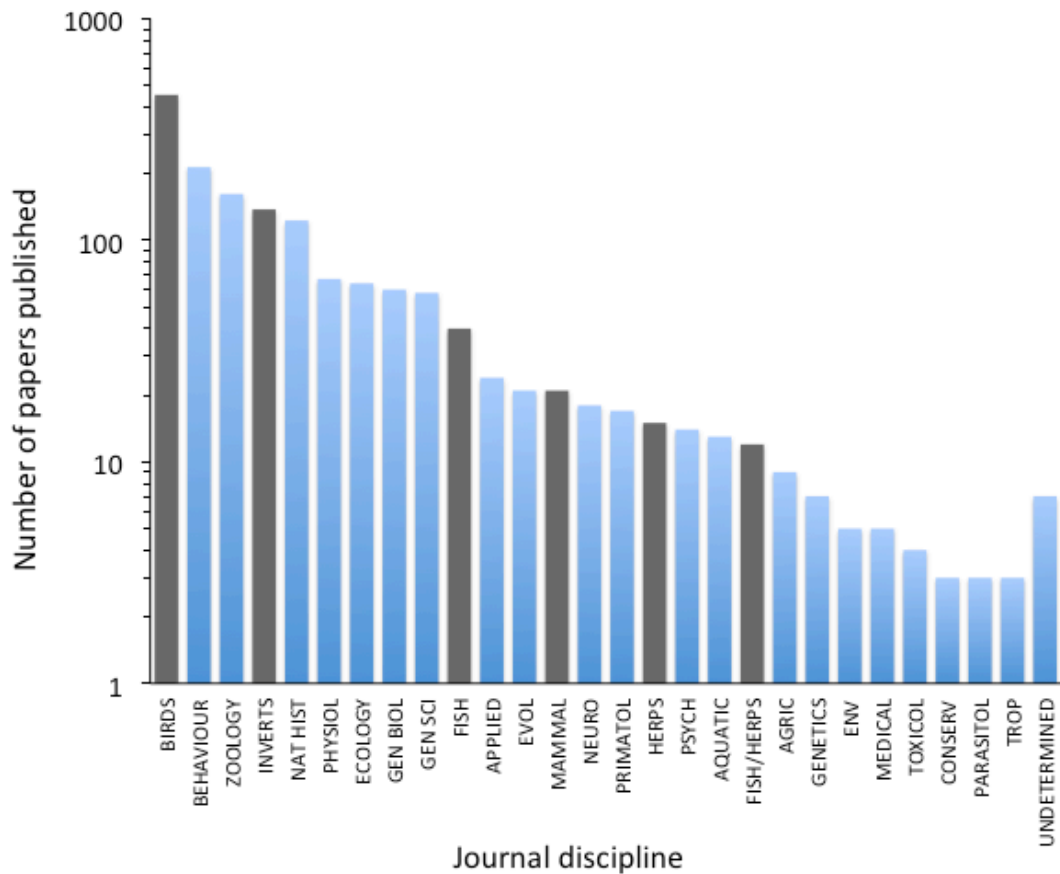


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859 **Figure 1.** The results of an analysis of primary research papers that focus on nest
860 building behaviour published in the fields of evolutionary biology, environmental
861 science, ecology and zoology between 1962 and 2012. (a) The number of published
862 research papers that primarily studied invertebrate, fish, amphibian, reptile, bird and
863 mammal nesting building behaviour. (b) The proportion of nest building research
864 papers published in successive 5-year periods that focused on invertebrate, fish,
865 amphibian, reptile, bird and mammals. See Appendix 1 for literature search and
866 analysis methodology. Note logarithmic scale of y-axis in both figures.

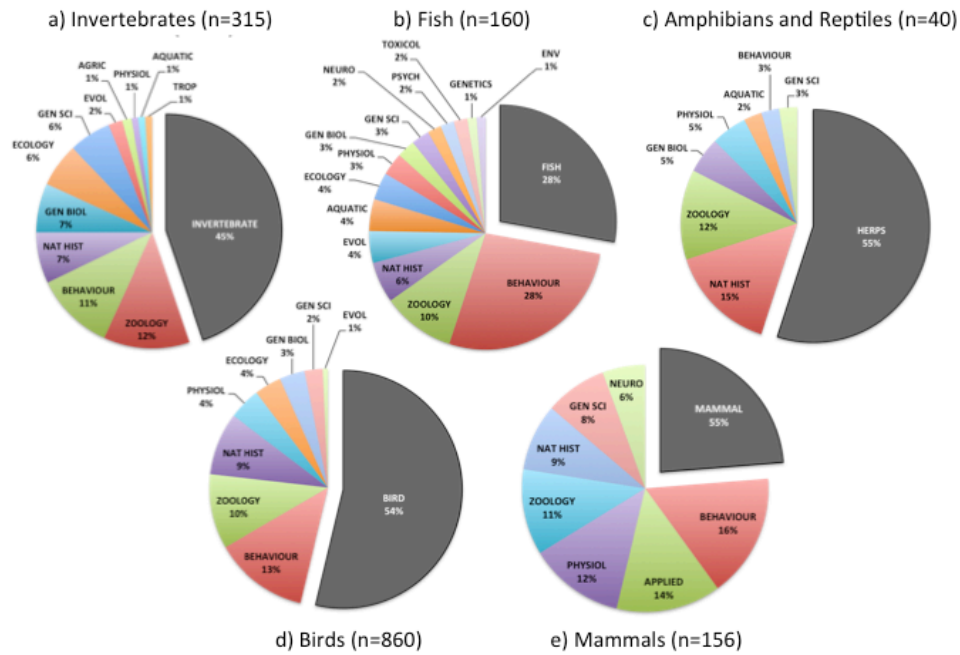
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870 **Figure 2** The results of an analysis examining the scientific fields of journals
871 publishing nest-building research. See Appendix Table 1 for details of journal fields
872 and associated journal titles. Note logarithmic scale of y-axis in both figures

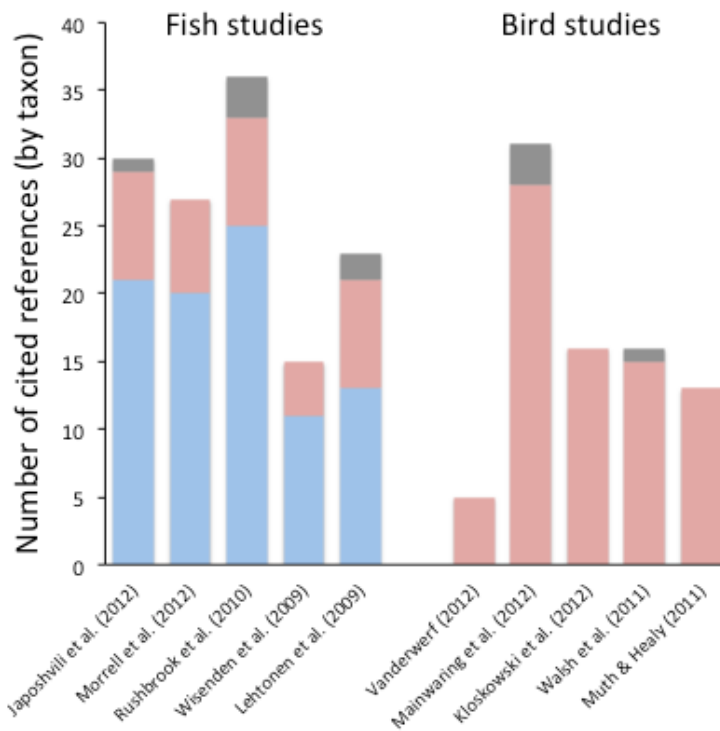
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875 **Figure 3.** The results of an analysis examining where researchers studying nest
 876 building behaviour publish their research findings. Separate pie charts represent the
 877 different taxonomic groups of nest building animals that are the focus of research,
 878 with the slices of each pie chart representing the disciplines of journals publishing the
 879 work. The proportion of papers published in taxon specific journals is shown slightly
 880 separated from each pie chart, and coloured dark grey. The propensity for nest
 881 building studies to be published in taxon-specific journals varies significantly across
 882 taxa ($\chi^2 = 51.227$, d.f.=4, $P < 0.0001$), with approximately twice the proportion of bird
 883 nesting behaviour studies being reported in taxon-specific journals than fish studies.

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886 **Figure 4.** The number of citations of fish (blue), bird (orange) and 'other' (mammals,
 887 invertebrates, herps; green) nesting behaviour papers that cited by five recent research
 888 papers drawn from the fields

889

890 **Appendix 1:** Methodology for literature review reported in the main paper
891 Research papers were gathered from the Web of Science online database using the
892 following search: Topic=("nest building" OR "nest construction") AND (behaviour OR
893 behavior)); refined by: Research Areas=(ENVIRONMENTAL SCIENCES ECOLOGY OR
894 ZOOLOGY OR EVOLUTIONARY BIOLOGY); Timespan=All Years (1950-present). The
895 search initially returned 1671 papers. Results were then individually screened and
896 edited to remove duplicate entries, secondary literature (reviews, book chapters) and
897 non-relevant papers, leaving the sample of 1582 papers that were included in the
898 analysis. Each paper was then coded for the primary taxonomic focus (I: invertebrates,
899 F: fish, A: amphibians, R: reptiles, B: birds, M: mammals), and for the journal discipline.