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

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Running head: Nest building in fish and birds
Abstract

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

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

Evolutionary, ecological and environmental aspects of nest building are studied in a wide variety of animals, from invertebrates to primates (Fig. 1a). In the fields of evolutionary and behavioural ecology, birds have proved exceptional models for the study of nesting behaviour, and avian studies dominate the literature; however, over
recent years there has been an increase in the number of research groups studying the
nest building behaviour of fish, and a concomitant increase in the number of fish
nesting publications (Fig. 1b).

1.1 Nest building fishes: who and how?

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

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

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

1.3 Aims of the review

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

2. Ecological adaptation and plasticity in nest construction

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

As endotherms, birds – and particularly small temperate passerines – expend a significant amount of energy in thermoregulation (Bartholm and Trost, 1970, Dawson et al., 1983, Nagy, 1987). Developing embryos and chicks are especially sensitive to both overheating and cooling (Webb, 1987) and can be exposed to rapid fluctuations in temperature as a result of diurnal and longer-term seasonal climatic changes. A primary function of bird nests is therefore to protect their contents from extremes of temperature (Hilton et al., 2004, Asokan et al., 2008, Heenan and Seymour, 2012).

Bird nests may also need to provide eggs and chicks with protection from precipitation – which can generate evaporative cooling effects – and cooling convection currents (Heenan and Seymour, 2012). A number of studies have demonstrated that birds are capable of adjusting the thermal qualities of nests in response to fluctuating environmental temperatures to maintain optimal nest microclimates. Both long tailed tits *Aegithalos caudatus* and blue tits *Cyanistes caeruleus* vary the mass of feathers incorporated into nests as ambient temperatures to ensure consistent thermal environment (McGowan et al., 2004, Mainwaring and Hartley, 2008). Recent investigations have also revealed that the mass of lining material incorporated into blue tit nests varies systematically along latitudinal clines in the UK, suggesting adaptive divergence in populations (Mainwaring et al., 2012).

By contrast, the physical properties of water means that aquatic environments provide a more buffered, thermally stable medium for nest building, at least over the typical lifetime of an active fish nest. Hence, thermoregulation is not an important factor influencing nest design in fish, although – because the speed of embryo development
in fish is closely tied to ambient water temperatures (Pepin, 1991) – spatial variation in temperature associated with water depth, shading or local water currents may influence nest site choice. Thermal regimes may also play an indirect role in nest construction in fish because dissolved oxygen (dO\textsubscript{2}) levels, which impact nesting behaviour and nest structure substantially (see 3.2 below), correlate closely and negatively with water temperature.

2.2 Dissolved oxygen

The bioavailability of oxygen is a far more important factor influencing the design and construction of fish nests than temperature per se. Although reduced oxygen levels may cause problems for offspring development in some cavity nesting birds such as woodpeckers (Ar \textit{et al.}, 2004), it is unlikely to pose a major limitation on design for most bird nests. In contrast, dissolved oxygen (dO\textsubscript{2}) levels can vary substantially both temporally and spatially in aquatic ecosystems, and the development of fish embryos is frequently oxygen-limited (Malcolm \textit{et al.}, 2010). Laying eggs into an enclosed nest that limits water movements means that in most cases nest building or cavity nesting fish species need to engage in fanning behaviour to waft oxygenated water over developing eggs, and this can constitute an energetically demanding and costly element of parental care (Jones and Reynolds, 1999a, Lissaker \textit{et al.}, 2003). There is also evidence that nest site choices, nest design and construction behaviour have evolved to mitigate the typically low and variable bioavailability of oxygen in aquatic environments. For example, bluegill sunfish \textit{Lepomis macrochirus} inhabiting ponds with spatially variable dO\textsubscript{2} levels choose well-oxygenated sites at which to build nests (Gosch \textit{et al.}, 2006).
Members of the sand goby group (*Pomatoschistus* spp.) are small marine fish that occupy shallow water habitats and typically build nests by excavating substrate from underneath empty bivalve shells and depositing it on top. Under conditions of low dO$_2$, male sand gobies *Pomatoschistus minutus* construct nests that have larger entrance holes than when under favourable dO$_2$ conditions, where males keep nest holes small to counter the threat of predation (Jones and Reynolds, 1999c, b, Lissaker *et al.*, 2003) or sexual competition from other males (Svensson and Kvarnemo, 2003).

Three spined sticklebacks alter the structure of nests through the nesting cycle; as embryos develop and have higher energetic demands, sticklebacks successively reduce the compactness of their nests (Wunder, 1930), presumably to enhance the availability of dO$_2$.

2.3 Coping with dynamic shearing forces

Both aquatic and terrestrial environments are subject to dynamic shearing forces generated by water and air currents, so both fish and birds may be required to select sheltered sites, robustly anchor nests, or otherwise construct nests that are resistant to these forces. Birds often fasten nests securely by weaving or knotting the nest material to supporting structures, and this is facilitated by precise control afforded by the use of the beak, which allows the fine manipulation required in such behaviour (Hansell, 2000). Although some fish, such as nine-spined sticklebacks *Pungitius pungitius*, are capable of performing simple weaving or ‘looping’ behaviour to attach their nests to submerged vegetation (Morris, 1958, Zyuganov, 1986), fish nests are more commonly placed in crevices or beneath rocks, or anchored to the substratum by the deposition of material (e.g. sand, fine gravel) on top. Some birds and fish use endogenous
secretions that act as glues and play an important role in anchoring nests. Some cliff-
nesting birds use such secretions to mix with nesting material to increase the
adhesiveness and/or structural rigidity of nests; this is perhaps exemplified most
extremely in Chinese swiftlets (genus *Collocalia*) which use mucus glycoproteins,
produced in the salivary gland, as a nest cementing substance that hardens in air
(Wieruszeski *et al.*, 1987). Sticklebacks secrete endogenous mucous-like glue –
named ‘spiggin’, after the Swedish for stickleback ‘Spigg’ (Jakobsson *et al.*, 1999) –
which facilitates the sticking together of nesting materials underwater. This glue is
produced in copious amounts in the kidney of sexually mature males and is coded for
by a family of genes that are closely related to vertebrate mucin genes (Jones *et al.*, 2001).

Fish can exhibit behavioural plasticity in nest construction in response to changes in
flow regimes. In an experimental study, designed to investigate the effects of
increased water flow rates on nest structure, individual male three spined sticklebacks
built smaller and more elongate nests – and incorporated more Spiggin per gram of
nest – than when building under no-flow conditions (Rushbrook *et al.*, 2010).
Similarly, under increasing water flow rates, male river blennies adjust the position of
nest entrance holes such that at the highest flow rates they face $180^\circ$ to the direction of
flow (Vinyoles *et al.*, 2002). Subtle adjustment of nest orientation in this species
ensures that the rate of water flow reaching the nest entrance remains remarkably
consistent, between 5-7 cm sec$^{-1}$, despite highly variable flow rates. A remarkably
similar behaviour is observed among lesser skylarks (*Alauda gulgula wattersi*), which
typically orient nest openings at $180^\circ$ to the direction of prevailing winds (Yuan,
1996). Many other birds also select nest sites that are sheltered from prevailing winds
and wind-driven precipitation; water pipits (*Anthus spinoletta*) in alpine tundra build
nests that are sunken into depressions (Boehm and Landmann, 1995) and in the Algerian Sahara, Houbara bustards (*Chlamydotis undulata undulate*) build nests under tufts of vegetation to provide shelter from northern winds (Gaucher, 1995).

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

### 2.4 The influence of predators and parasites

Both terrestrial bird nests and those built by fishes underwater are subject to exploitation by a wide range of predators and parasitic organisms, though the nature of these threats varies both between and within nesting taxa. Predators impose particularly strong selection on nest site choices, nest construction behaviour and nest design in birds (Lima, 2009). For example, the concealment of eggs with nest material shown by mallards *Anas platyrhynchos* has been demonstrated to significantly reduce the risk of nest predation (Kreisinger and Albrecht, 2008) and the choice of pebble colouration in the simple nests of piping plovers also plays a role in camouflaging the
clutch (Mayer et al., 2009). Siberian jays *Perisoreus infaustus* show significant changes in nest site preferences after artificial manipulation of perceived predation threat via playback of predator calls, selecting increasingly protected nest sites (Eggers et al., 2006). In an almost directly analogous study in sticklebacks, the presence of egg predators induces preferences for structurally complex nest sites (i.e. in vegetation) over generally preferred open sites (Candolin and Voigt, 1998).

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

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

Nests primarily serve as functional receptacles for developing eggs and offspring, and so it is not surprising that females often exhibit preferences to lay eggs in nests that
are ‘fit for purpose’. Accordingly, female penduline tits *Remiz pendulinus* show
preferences for larger better insulated nests (Hoi *et al.*, 1996), and benefit by doing so
because they can invest less time in incubating the eggs (Grubbauer and Hoi, 1996).
Similarly, female red bishops *Euplectes orix* preferred male-built nests that were
woven more densely and had more overlapping entrance roofs, traits related to nest
durability (Metz *et al.*, 2009).

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

In the simplest case, nest size in fish can indicate body size, as in the corkwing wrasse
*Symphodus melops* (Uglem and Rosenqvist, 2002). Barber *et al.* (2001) provided
some of the first data that the structure of male-built nests might convey other useful
information to female fish, since male three-spined sticklebacks with greater levels of
kidney hypertrophy – indicative of circulating androgen levels – built nests that were
neater and more compact. In sticklebacks, the kidney is the site of nesting glue
(‘Spiggin’) biosynthesis (Jakobsson *et al.*, 1999), so one explanation is that males
with larger kidneys build higher quality nests at least partly because they have an
abundance of glue to stick together nesting materials. In an experimental study of
marine fifteen-spined sticklebacks *Spinachia spinachia*, the number of glue threads
secreted into nests was related to feeding ration; males fed higher rations incorporated
more threads, suggesting that nest composition may reflect energetic status, which in
turn might indicate their parental ability. Further, when choosing among males that
had been fed similar rations, female fifteen-spined sticklebacks preferred to lay eggs
in nests containing more threads, suggesting that females use cues from the nest to
make spawning decisions (Östlund-Nilsson, 2001). Evidence that variation in male
nest building behaviour might give information to females about male quality also
comes from studies examining the effect of debilitating parasite infections. Among
sticklebacks infected with the parasitic cestode *Schistocephalus solidus* – which
depletes host energy reserves and reduces circulating androgen levels (Barber et al.,
2008, Macnab et al., 2011) – nest building is most severely affected amongst males
harbouring the largest worms (Rushbrook and Barber, 2006, Rushbrook et al., 2007,
Macnab et al., 2009). By basing their choice of mates on attributes of the nests they
construct, females may therefore avoid the most heavily parasitized, or otherwise
energetically challenged males.

In *Pomatoschistus* spp. gobies, the amount of sand deposited on top of the nest is
uncorrelated with male body size (Svensson and Kvarnemo, 2005), but it is condition-
dependent, and so may honestly signal male quality. In experimental studies, male
common gobies *P. microps* held in tanks without access to prey were less likely to
construct nests (Jackson et al., 2002), and male sand gobies fed on higher rations built
bigger nests (Olsson et al., 2009). Female gobies typically show preferences for nests
with more deposited sand (Svensson and Kvarnemo, 2005, Lehtonen and Lindstrom,
2009, but see Lehtonen and Wong, 2009), which may give protection against
predators (Lindstrom and Ranta, 1992). When given a choice between males that

differed in body size and nest size, females showed the strongest preference largest

nests as long as they were built by large males, suggesting that females use nest size

as one of a number of multiple cues in this species (Lehtonen et al., 2007).

Some fish construct elaborate ‘bowers’ – display arenas that have no nest function –

that appear to fulfil an identical role to those constructed more famously by birds (e.g.

Borgia, 1985). In Lake Malawi, a number of genera of cichlids construct volcano-

shaped sand bowers, and there is substantial evidence that physical aspects of bowers

are repeatable, reflect the quality of individual builders (Schaedelin and Taborsky,

2006, Martin and Genner, 2009) and are used by females to choose males (Kellogg et

al., 2000, Genner et al., 2008, Young et al., 2010). Although there is some

certainty over the use of the term ‘bower’ to describe these artefacts, since these

cichlids are mouth-brooders that do not construct a separate nest (Tweddle et al.,

1998), the important point is that the design of the display arena is essentially

unrelated to by any nesting function. The existence of artefacts created purely for

display purposes by fish therefore raises the possibility that some attributes of

functional nests may also serve a purely ornamental purpose. Sticklebacks, for

example, are known to incorporate non-structural decorations into their nests, with

impacts on mate choice. Östlund-Nilsson & Holmlund (2003) demonstrated that male

marine three-spined sticklebacks used ornamental threads, provided at low frequency

by the experimenters, to decorate their nests and that females subsequently preferred

nests that incorporated these decorations. Furthermore, the artificial addition of

brightly coloured threads to three-spined stickleback nests located in the field

increased both the level of a male’s courtship and his investment in nest building, and

in the lab led to males building neater and more compact nests (Morrell et al., 2012).
These results suggest that the energy saved by having an artificially enhanced nest can be reinvested in other aspects of courtship.

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

Understanding the extent to which animals are able to alter their behaviours to cope with human induced rapid environmental change (HIREC), and determining the fitness consequences of such behaviour changes, has become a key topic in evolutionary ecology (Sih et al., 2011, Candolin and Wong, 2012). The impact of HIREC is increasingly a focus of nest building research, in both birds and fish. In birds, nesting responses to introduced predators can be affected. On the Hawaiian island of Oahu, the height at which a forest-dwelling monarch flycatcher (Chasiempis ibidis) built their nests increased from 7.9m to 12m between 1996 and 2011 (Vanderwerf, 2012). The fact that this population level change was not reflected by the behaviour of individuals – which did not change their nest height over successive breeding seasons – suggests a rapid evolutionary rather than a learned response to predation threat. In other cases individual plasticity in behaviour can ‘rescue’ certain species in the face of acute environmental changes; however, not all behavioural changes are likely to be adaptive. ‘Ecological traps’ arise where normally adaptive responses lead to maladaptive outcome in anthropogenically altered environments (Schlaepfer et al., 2002). In birds, there are a number of documented cases of species making poor nest site choices in altered environments. For example, Northern cardinals (Cardinalis cardinalis) nesting in exotic shrubs including honeysuckle Lonicera sp., incurred significantly higher losses to predators than those nesting in...
native shrubbery, as a likely result of sub-optimal plant architecture and leaf
phenology (Rodewald et al., 2010).

Degradation of aquatic ecosystems can result from physical habitat destruction,
altered environmental temperatures (as a result of global warming and/or direct input
of effluents from industrial cooling processes), altered flow regimes and species
introductions. Furthermore, aquatic ecosystems act as sinks for nutrients from
agricultural runoff and a wide variety of anthropogenic chemicals, including those
with endocrine disrupting actions that affect fish sexual maturation and reproductive
behaviours, including nest construction (van der Sluijs et al., 2011). There is
increasing interest in the effect of changing environments on fish reproductive
behaviour, including nesting behaviour, and a growing body of work examining the
impacts of eutrophication (Candolin, 2009). In sticklebacks, increased algal growth
creates both greater availability of nesting material and increased numbers of nesting
opportunities for sticklebacks (Candolin, 2004, Candolin and Salesto, 2006), meaning
that even poor quality individuals in the population may be able to build nests
(Heuschele and Candolin, 2010). In such environments, variation in the numbers of
eggs acquired by nest-holding males is lower than in non-eutrophic areas, suggesting
that females may be less discriminating in their mate choice (Candolin, 2004).
Increased opportunities for nesting may therefore reduce overall levels of selection in
human impacted habitats. An important side effect of eutrophication, as vegetation
begins to decay, is the depletion of dO2, with knock-on consequences for nesting
behaviour (see 3.2 above).

Because of their solubility in water, anthropogenic chemicals often impact aquatic
organisms more immediately than birds, and there is considerable interest on the
effects of chemicals that have endocrine disrupting action in the reproductive biology
of fish (Jobling et al., 1998). Nest building behaviour in fish is highly sensitive to such pollutants, with a wide variety of chemicals – including the natural human estrogen 17β estradiol, synthetic estrogens used in the contraceptive pill, plasticisers such di-N-butyl phthalate and anti-androgenic cancer drugs such as flutamide – all having significant effects on the nest building behaviour of sticklebacks or gobies (Wibe et al., 2002, Sebire et al., 2008, Saaristo et al., 2010, Aoki et al., 2011, Sebire et al., 2011). The reproductive behaviour and physiology, including nest construction and the production of the nesting glue Spiggin, is now widely used as a bioassay for quantifying the sub-lethal effects of anthropogenic chemicals in aquatic environments (Sebire et al., 2008, OECD, 2011).

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

It is clear that there is significant overlap in the questions being addressed by researchers investigating nest construction in birds and fish, and that many of these questions – particularly regarding the fitness consequences of behavioural responses to changing environments – require urgent attention. In addressing questions of such general importance, it is imperative that the results of research being undertaken across the taxonomic spectrum are fully utilised. Unfortunately, in the case of nest building behaviour, there is only limited evidence that such taxonomic boundaries to knowledge are being broken down (Fig. 3). An analysis of literature cited in recently published studies on the nesting behaviour of fish and birds, covering topics of broad general interest, reveals that there is limited reference to non-focus taxa, and it seems that the crossing-over of knowledge from fish and bird studies may be asymmetrical, with fish-focused papers more likely to cite bird literature than vice versa (Fig. 4).
Birds and fish both provide excellent models for the scientific study of nest building; however, they are unlikely to be equally well suited for addressing all questions. Because of their terrestrial nesting habits, the possibility for tracking the survival and reproductive success of offspring in natural field conditions, and the existence of long-term study sites, birds are likely to prove better models for studying the fitness consequences of variation in nest construction or nest structure. In contrast, the many difficulties of studying the reproductive success of fish under natural conditions impose a significant constraint on their use for such studies. Conversely, the small number of offspring produced by birds in a single season largely prohibits the use of quantitative genetic techniques that might otherwise be used to partition the variance in nest construction attributable to genetic and environmental factors. Such techniques are extremely data-hungry and require the production of large numbers of known-pedigree, closely-related offspring (Wilson et al., 2010), and they can be used successfully to identify genetic effects on behaviour in fish (Dingemanse et al., 2009, Dingemanse et al., 2012) and specifically to examine genetic effects on nest building behaviour in turtles (McGaugh et al., 2010). Although the repeatability of nest building behaviour can be studied in fish and birds that build successive nests (Rushbrook et al., 2008, Walsh et al., 2010, Japoshvili et al., 2012), future studies that seek to identify the genetic basis of variation in nest building behaviour are likely to be most successfully undertaken in fish models.

Almost all bird species construct nests, so they provide an excellent model for undertaking both large-scale phylogenetic studies of nest construction behaviour (Collias, 1997) and finer scale studies to examine interrelationship between species (Collias and Collias, 1972, Zyskowski and Prum, 1999, Kirwan et al., 2010). Such studies are greatly facilitated by the availability of bird nest collections in museums.
Nest building is more sparsely distributed across teleost fishes, however, and phylogenetic approaches have been limited to examining the evolution of nest building per se (Hanel et al., 2002, Mank et al., 2005), rather than the types of construction behaviour that have evolved, or of using nest architecture as a means of informing relationships between species.

One final reason for developing fish as models for examining questions of general interest in nest building behaviour is related to the welfare concerns surrounding the use of higher vertebrates in scientific research. The 3Rs principles of reduction, refinement and replacement in the use of animals in scientific research (Russell and Burch, 1959) are increasingly advocated, and guidance issued by NC3Rs and similar organisations stipulates that research questions should be addressed “using species that are most likely to produce satisfactory results with the least degree of harm to the animals involved” (Anon, 2008). Most contemporary research on nest building behaviour can be carried out with minimal harm or stress to subjects, and modern field and experimental behavioural scientists strive to implement the highest standards of ethical treatment of study animals. However, where there is a requirement to examine the effects of environmental stressors on nesting behaviour, or to carry out invasive or terminal procedures to better understand – for example – the neurological control of nesting behaviour (Sager et al., 2010), researchers should seek to identify the lowest useful taxonomic group for study. Although there continues to be significant discussion over the consciousness or otherwise of fishes, and their ability to suffer and/or perceive pain (Rose, 2002, Sneddon et al., 2003, Huntingford et al., 2006, Braithwaite, 2010), ‘lower’ vertebrates – including fish – might ultimately prove to be more suitable model systems than ‘higher’ vertebrates such as birds for examining basic questions about nest building behaviour under laboratory conditions.
In conclusion, although biologists investigating the nesting behaviour of birds and fish may often do so to inform the ecology or biology of a particular species – for example with a view to improving its conservation status – it is increasingly the case that studies are undertaken to test more general hypotheses that are of interest and importance across taxonomic boundaries. There is, however, only limited evidence that major findings of studies on fish nesting behaviour are informing contemporary bird studies, and *vice versa*. I hope that this short review may therefore be used as a jumping-off point for bird biologists who may be interested in learning more about the nesting behaviour of fish, and that it may stimulate fish biologists to find out more about contemporary nest building research in birds and other taxa.

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Figure 1. The results of an analysis of primary research papers that focus on nest building behaviour published in the fields of evolutionary biology, environmental science, ecology and zoology between 1962 and 2012. (a) The number of published research papers that primarily studied invertebrate, fish, amphibian, reptile, bird and mammal nesting building behaviour. (b) The proportion of nest building research papers published in successive 5-year periods that focused on invertebrate, fish, amphibian, reptile, bird and mammals. See Appendix 1 for literature search and analysis methodology. Note logarithmic scale of y-axis in both figures.
Figure 2 The results of an analysis examining the scientific fields of journals publishing nest-building research. See Appendix Table 1 for details of journal fields and associated journal titles. Note logarithmic scale of y-axis in both figures.
Figure 3. The results of an analysis examining where researchers studying nest building behaviour publish their research findings. Separate pie charts represent the different taxonomic groups of nest building animals that are the focus of research, with the slices of each pie chart representing the disciplines of journals publishing the work. The proportion of papers published in taxon specific journals is shown slightly separated from each pie chart, and coloured dark grey. The propensity for nest building studies to be published in taxon-specific journals varies significantly across taxa ($\chi^2 = 51.227$, d.f.=4, P<0.0001), with approximately twice the proportion of bird nesting behaviour studies being reported in taxon-specific journals than fish studies.
Figure 4. The number of citations of fish (blue), bird (orange) and ‘other’ (mammals, invertebrates, herps; green) nesting behaviour papers that cited by five recent research papers drawn from the fields.
Appendix 1: Methodology for literature review reported in the main paper

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