

Context-dependent resource choice in a nest-building fish

Abstract

When making decisions, individuals can be influenced by both the range of options available to them and intrinsic factors, such as their own body size or condition. The current understanding of the topic comes mostly from studies of foraging behaviour and mate choice, whereas other fitness-related decisions have been the subject of much less attention. Here, we investigated how the number of available options, along with body size and condition, affect the nesting resource choices of male sand gobies, *Pomatoschistus minutus*. The results show that resource choices were not affected by additional choice options (i.e. binary vs. ternary choice situation) or the body condition of the chooser, whereas resource size, resource type (i.e. whether choices were between arched or flat shaped resources) and body size did have an effect. In particular, while larger nesting resources were chosen more often in most situations, this pattern was stronger among larger males and when the resources had a flat, rather than arched, shape. Indeed, in the case of arched resources, the medium size category was more popular than the smaller and the larger one. Together, the results show that both intrinsic and extrinsic factors can influence important behavioural decisions over resource choice.

Keywords:

body condition, body size, comparison, context dependent, decision making, nest, option, parental care, resource choice, sand goby

INTRODUCTION

Optimality-oriented theories predict that animals respond to the costs and benefits of a choice situation by making optimal behavioural decisions. However, empirical evidence shows that behavioural decisions can vary–both among and within individuals–much more than predicted by the optimality approach (Bateson, Healy, & Hurly, 2003; McNamara & Houston, 2009; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). One reason for this variability is that the choices animals make can be context-dependent, especially if the decision-making process involves comparisons (Bateson & Healy, 2005; McNamara & Houston, 2009). In some cases, individuals have been found to be sensitive to the number or types of alternatives that are available to them (Bateson et al., 2003; Bateson & Healy, 2005; Nevai, Waite, & Passino, 2007). For example, attractiveness of a potential mate may not necessarily be a direct function of his/her underlying quality, but instead, could depend on the other available suitors with whom he/she is being compared (Bateson & Healy, 2005).

Choices that individuals make may not only depend on the specific options that are available to them, but can also be influenced by intrinsic factors, sometimes referred to as the chooser's 'state' (Wolf & Weissing, 2010; Fawcett, Hamblin, & Giraldeau, 2013). For example, body condition and body size can both affect the decisions and choices that individuals make (Gross, 1996; Bateson & Healy, 2005; Lehtonen, Lindström, & Wong, 2015). In this regard, our understanding of how the decision-making process is related to both extrinsic (especially range of choice options) or intrinsic factors (e.g. body condition, size) come mostly from studies of foraging behaviour, or, in the context of reproduction, from studies of mate choice (Bateson et al., 2003; Bateson & Healy, 2005; Hutchinson, 2005). By contrast, the relative effects of the choice options and intrinsic factors in other fitness-related decisions (including other reproductive contexts) have been the subject of much less theoretical and empirical attention. However, such decisions, for example in the contexts of oviposition and nesting site choice, can have a profound impact on offspring success (Kraak, Bakker, & Hočevar, 2000; Brown & Shine, 2005; Natsumeda, 2005; Byrne & Keogh, 2009; Barber, 2013; Reedy, Zaragoza, & Warner, 2013; Mainwaring, Hartley, Lambrechts, & Deeming, 2014). Decisions over resources needed for nesting, such as suitable nesting holes or nest-building materials, could be similarly important and affected by the range of options available to the nesting individual, as well as the nest builder's intrinsic properties.

The sand goby, *Pomatoschistus minutus*, is an ideal model with which to test how nesting decisions may be affected by both the range of nesting resource options available for choice and the nest builder's intrinsic properties. To build a nest, a male sand goby requires a nesting resource, such as an empty mussel shell or flat stone (Lindström, 1988; Lehtonen & Lindström, 2004). In most cases, the male piles sand on top of, and excavates under, the nesting resource, leaving a single narrow opening. Hence, the size and shape of the resource the male acquires directly impacts the nest-building process and the size and appearance of the completed nest. The nest holder then tries to attract females to lay eggs (in a single layer) on the ceiling of the nest and, if successful, the male takes exclusive care of the eggs by nursing and guarding them. A male can guard multiple egg clutches simultaneously (Lindström, 1988, 1992). The size of his nesting resource can influence both his attractiveness to females (Lehtonen, Rintakoski, & Lindström, 2007) and the number of eggs he physically can receive, i.e. his mating success (Lindström, 1988). However, bigger is not necessarily better: occupying a large nesting resource is also likely to be associated with costs, such as the need to use more sand for covering the resource, circulation of larger volumes of water when aerating eggs in the larger nest, or defending the nest and eggs against usurpation, parasitic fertilisations and potential egg predators (Kvarnemo, 1995;

Lindström & Pampoulie, 2005; Lehtonen, Vesakoski, Yli-Rosti, Saarinen, & Lindström, 2018). Interestingly, males were found to prefer a large nesting resource in the presence of a second, smaller alternative (Wong, Lehtonen, & Lindström, 2008; Lehtonen, Lindström, & Wong, 2013; Flink & Svensson, 2015), whereas some studies presenting sand gobies with a choice of three different sized resources have found a preference for the intermediate option (Kvarnemo, 1995; Japoshvili, Lehtonen, Wong, & Lindström, 2012; Lehtonen, Wong, & Kvarnemo, 2016). These results may be driven by the relative sizes of the resources on offer (albeit these have been fairly consistent among the studies), complexity of the demands of parental care and nest defence, or how the choice of resource is affected by the range of options available to the chooser. However, whether nesting resource choice is indeed affected by the range of available options is not known.

Here, we experimentally tested whether a male's choice of nesting resource size is affected by the range of options, the type of the resource, or the nest builder's body condition and size. If nesting resource choice is, indeed, relative in the sense that it is influenced by the range of options available to the chooser, based on earlier work on context-dependent choice (as cited below), we can make the following three predictions with regard to resource size. First, we may expect the difference in relative popularity of a small vs. medium-sized resource to be smaller in a binary choice situation than when an even larger option is also offered (i.e. when a small, medium and large resource are available; see Tversky & Simonson, 1993). Second, we may also expect a medium-sized resource to be chosen less often in relation to a large one when males are given a binary choice between these two options, compared to when all three size options are available (Tversky & Simonson, 1993; Schuck-Paim, Pompilio, & Kacelnik, 2004; Fawcett et al., 2013). Third, we may expect that the relative difference in the popularity of the more "extreme" choice options, here a small vs. a large resource, is reduced when an intermediate (here: medium-sized) option is also present (Huber, Payne, & Puto, 1982; Doyle, O'Connor, Reynolds, & Bottomley, 1999; Sedikides, Ariely, & Olsen, 1999; Bateson et al., 2003).

Aside from resource size, different kinds of nesting resources can affect offspring fitness or the chooser's perception of the resource's desirability, as shown, for example, in blue tits, *Cyanistes caeruleus* (Møller et al., 2014). Therefore, our fourth prediction is that resource choice may be affected by the architecture of the resource being offered (arched vs. flat, see Methods for details). Finally, we tested the effects of two important 'state' measures, i.e. body condition and body size, on nesting resource choice. In this regard, our fifth prediction is that, due to the costs related to holding a large nest (sand gobies: see above; number of bird species: Mainwaring et al., 2014), males in poorer condition should choose smaller nesting resources (relative to their size) compared to higher condition males.

METHODS

The study was conducted at the Tvärminne Zoological Station (59°50.7´ N; 23°15.0´ E) in 2016 during the sand goby breeding season, which, in the northern Baltic Sea, peaks from late May to early July.

To capture males for our experiment, we placed artificial nesting resources on the sandy substrate in a shallow water habitat near the field station (Vargskär). Males that had built a nest (or at least initiated nest building) using these nesting resources were later caught with the aid of a mask, snorkel and hand nets, and then immediately transported to the field station. To increase variation in the size of captured males, similar numbers of the following four kinds of nesting resources were used: two sizes of clay flowerpots (maximum diameter width and length of small pot: 4.5 cm and 4.2 cm; large: 8.3 cm and 8.2 cm) and two sizes of ceramic tiles (length × width of small: 5.0 cm × 5.0 cm; large: 9.9 cm × 9.9 cm). Halved flowerpots and ceramic tiles were chosen to simulate natural nesting resources, both of which are readily accepted by sand gobies in the field (flowerpots: Lindström & Pampoulie, 2005; tiles: Wong, Lehtonen, & Lindström, 2018) and under laboratory conditions (Lehtonen et al., 2018).

Back at the field station, males were first kept for a short period (less than a week) in holding aquaria of ~100 litres (with max 20 individuals in each), and fed live mysid shrimp (*Neomysis integer*) *ad libitum*. All stocking and experimental aquaria (see below) were placed in a non-insulated greenhouse and supplied with a continuous through-flow of water, pumped from the Baltic Sea. Hence, the aquaria were subject to natural water conditions and day/night cycles.

After completion of each trial (see below for details), the focal male was weighed to the nearest 0.01 g in a container of water on an electronic balance, and its total length was measured to the nearest 0.5 mm on a measuring board with a grid scale. In total, $N = 346$ males were tested (total length: 50.4 ± 0.5 mm [mean ± standard error], weight 1.00 ± 0.02 g, $N = 341$ males successfully measured). The males were randomly distributed among the different choice scenarios (i.e. treatments, see below). No individual was used more than once. The randomisation was done on a daily basis so that, as far as possible, a similar number of replicates of all treatments were run at the same time. All randomisation in the experiment was achieved with a random number generator (available at https://www.random.org/).

Choice between small vs. medium, in the presence or absence of a large resource

We first assessed choices between small- and medium-sized nesting resources in a binary choice situation, as well as in another treatment in the presence of a large nesting resource (see below and Figure 1 for details regarding the nesting resources). If the context of the choice situation affects resource choice of sand goby males, we would expect that the medium option, compared to the small one, is chosen less often when the large option is also available (Tversky & Simonson, 1993).

The choice arenas (aquaria) measured 68 cm × 25 cm × 22 cm (length × width × height of water level), and had a 4 cm layer of fine sand covering the bottom. The nesting resources were randomly assigned to the left, right and centre of the arena. When only two nesting resource options were available (here: small and medium), one of the three possible positions where the resource could have been placed within the aquarium (left, right or centre) was left empty in a randomised fashion (Lehtonen et al., 2016).

Each replicate was initiated by placing a sand goby male into an experimental tank. He was then given up to 48 hours to start building a nest and the replicate was terminated if no nest building took place within that time. All tanks were checked ~7 times daily between 08:00 and 23:00 to record male location and any signs of nest building. The male was considered to have chosen a nesting resource when it had started to pile sand on top of, and excavate under, the nesting resource (as per Lehtonen et al., 2013, 2016). After the first signs of nest building were observed, the male was left in the tank for a further ~18 hours. In some cases, the male initiated building of more than one nest, in which case we determined the male's resource choice as the option with which he had associated with most frequently (as per Japoshvili et al., 2012; Lehtonen et al., 2016; Lehtonen & Wong, 2020).

The two treatments (binary: small vs. medium resource, and ternary: small vs. medium vs. large) were run with nesting resources of two different kinds (hereon: architecture): halved terracotta flowerpots (hereon: 'arched nesting resources') and ceramic tiles (hereon: flat nesting resources). The dimensions of the small (hereon: S), medium (hereon: M) and large (hereon: L) arched and flat nesting resources are given in Figure 1. The sizes were chosen so that nesting resources of the two architectures, arched and flat, matched in surface area in all three size options (S, M and L). This is important because the surface area of the roof of the nesting resource acts as a physical limit on male mating success by determining the maximum number of eggs a male can potentially hold in the nest (Lindström, 1988, 1992). However, within a replicate, only nesting resources of the same architecture (arched or flat) were used. In replicates with arched nesting resources, the nesting resources were facing the front of the aquarium, whereas all four sides of each flat nesting resource were identical.

We completed 110 (N_{arched} = 39, N_{flat} = 71) and 73 (N_{arched} = 36, N_{flat} = 37) replicates for the S vs. M and S vs. M vs. L treatments, respectively. The focal male made a choice between the given options in 65 (N_{arched} = 33, N_{flat} = 32) replicates in the S vs. M treatment and 64 (N_{arched} = 32, N_{flat} = 32) replicates in the S vs. M vs. L treatment. Barnard's exact test (Barnard 1945) was used to compare the relative popularity/attractiveness of S and M nesting resources in the two choice situations ('Barnard' package in R, two-sided test).

Choice between medium vs. large, in the presence or absence of a small resource

We were also interested in testing whether the presence vs. absence of a S nesting resource would increase the relative attractiveness of the M option relative to the L. Notwithstanding resources sizes, the replicates were run as described above.

We completed 82 M vs. L binary choice replicates (N_{arched} = 36, N_{flat} = 46), with the focal male making a choice in 68 (N_{arched} = 34, N_{flat} = 34) of those replicates. We also used the same N = 73 S vs. M vs. L replicates as above. Barnard's exact test (two-sided) was again used to compare the relative popularity of M and L nesting resources in the two choice situations.

Choice between small vs. large, in the presence or absence of a medium resource

We next tested the hypothesis that the availability of a third, intermediate option (M nesting resource), may decrease the attractiveness difference between the two extreme (S and L) options observed in a binary choice situation, especially when the options differ non-linearly in at least two attributes (Huber et al., 1982; Doyle et al., 1999; Sedikides et al., 1999; Bateson et al., 2003). Here, we assume such a multimodal asymmetry to exist with regard to different sized arched–and possibly also flat–nesting resources. In particular, we expected the curvature of arched nesting resources (Figure 1, Figure 2a) to affect the costs of nest building and maintenance (detailed in the introduction) in a non-linear fashion. Specifically, it is intuitive that the costs of nest defence (e.g. the number and intensity of aggressive interactions) and maintenance (e.g. sand piling and nest entrance adjustments) should increase non-linearly with nesting resource size, while the male's maximum mating success (with regard to the area available for eggs to be laid; Lindström, 1988) should increase in a more linear fashion. Accordingly, we compared the relative popularity of S and L nesting resources in a binary situation ($N = 81$, with the focal male making a choice in $N_{arched} = 33$ and $N_{flat} = 33$ replicates) as well as in the presence of the M option (S vs. M vs. L choice scenario, the replicates were the same as above, $N = 73$).

Effect of resource architecture

To assess the effect of resource architecture (arched or flat) on the decisions of sand goby males, we combined the data from the above treatments, using all males that made a choice and for which we had both total length and body mass measures ($N = 260$). In particular, we applied an ordinal regression, in which the size of the chosen resource (S, M or L) was the response variable, with the order S < M < L being assumed (package 'ordinal' and function 'clm' in R). Because the analysis was run over the entire data-set, the choice options used in each replicate (S vs. M / S vs. L / M vs. L / S vs. M vs. L) was added as a factor. In addition, hypotheses regarding body condition and body size (see 'Effect of body size and body condition', below) were assessed in the same model, and these were also added as effects (see below for details). For the simplicity of interpretation, we were only interested in the main effects. Their significance was tested by removing the effect of interest from the main model and then comparing the two models with a log-likelihood test (as per Crawley, 2007).

If resource architecture was found to have a significant effect, we proceeded to compare the distribution of choices between arched and flat resources in separate tests for each of the choice scenarios (Barnard's exact for S vs. M, S vs. L and M vs. L, and Pearson's Chi-squared for S vs. M vs. L).

Effect of male body size and body condition

To test whether body size or body condition affects nesting resource choice, these were added as effects in the above-described ordinal regression model. Specifically, we used total length as a proxy for body size and 'scaled mass index' as a proxy for body condition. We established the latter following the procedure described by Peig & Green (2009). Briefly, this involved establishing a standardised major axis regression using the 'smatr' R package (Warton, Warton, Duursma, Falster, & Taskinen, 2012). To calculate the scaling coefficient beta that was needed to describe the relationship between male total length and body mass in this population of sand gobies, we used all the males in the study for which we had both measures, independent of whether they had made a choice (N = 341). To increase the accuracy of the estimate, we also used N = 215 additional males that were measured during the same field season (resulting in beta = 3.09).

Ethical note

The behavioural choice experiments carried out in this study were non-invasive and reflected the kinds of choice behaviours that sand gobies would make in the wild. After the completion of trials, fish were either retained for future, unrelated studies or returned to the sea on the same day. The study was approved by ELLA, the Finnish Animal Experiment Board (ESAVI/3915/04.10.07/2016).

RESULTS

Choice between small vs. medium, in the presence or absence of a large resource

Sand goby males' relative choice between S (i.e. small-sized) and M (i.e. medium-sized) nesting resources in the binary (only these two options present) and ternary (also L option present) choice situations did not differ significantly (Barnard's exact test, $P = 0.56$; Figure 2b).

Choice between medium vs. large, in the presence or absence of a small resource

For the comparison of the binary choice scenario between M and L nesting resources with the choice situation having also a S resource as a third option (ternary choice), we found that the presence of the S option did not have a significant effect (Barnard's exact test, $P = 0.72$) on the relative popularity of the M and L resource options (Figure 2c).

Choice between small vs. large, in the presence or absence of a medium resource

When we compared the binary choices between a S and L nesting resource and replicates in which males made the same choice in the presence of a M option, we found no significant effect of the availability of the M option on the relative popularity of the S vs. L options (Barnard's exact test, $P = 0.12$; Figure 2d).

Effect of resource architecture

As expected, the sizes of the options on offer affected whether a smaller or larger option was chosen (ordinal regression, log-likelihood significance test: $\chi^2_3 = 121.4$, $P < 0.001$). The architecture (arched vs. flat) of nesting resources also had a significant effect on the size of the resource males chose (ordinal regression, log-likelihood significance test: $\chi^2_1 = 34.42$, $P < 0.001$). To better understand this overall effect of resource architecture, we then assessed the effect separately for the four different choice scenarios (Figure 3). This approach revealed that nesting resource choice did not significantly differ between arched and flat resources when the options were S vs. M (Barnard's exact test: $P = 1.0$; Figure 3a). However, arched and flat nesting resources had a tendency to differ under the S vs. L choice scenario, and they differed under the remaining 2 choice scenarios. In particular, there was a marginally non-significant tendency towards the S option being chosen more often (relative to M) when the nesting resources were arched as opposed to flat (Barnard's exact test: $P = 0.057$; Figure 3c). In the case of M vs. L choice options, the M option was chosen more often when the nesting resources were arched (Barnard's exact test: $P < 0.001$; Figure 3b). Finally, the choices between all three nesting resource sizes (S, M and L) also differed between arched and flat resources, with the L option being chosen more often in the latter case (Pearson's Chi-squared test: $\chi^2_2 = 11.67$, $P = 0.003$; Figure 3d). Hence, when both M and L options were available, M was more popular than L in the case of arched nesting resources, whereas the preference was the opposite for flat nesting resources (Figure 3). More generally, the relative popularity of the L option was lower when nesting resources were arched, as compared to when the nesting resources were flat (Figure 3).

Effects of male body size and body condition

The ordinal regression model showed that male total length had a significant effect on choices (ordinal regression, log-likelihood significance test: $\chi^2_1 = 7.615$, $P = 0.006$): larger males chose larger nesting resources. In contrast, scaled mass (as a proxy of body condition) did not have a significant effect (ordinal regression, log-likelihood significance test: $\chi^2_1 = 0.1228$, $P = 0.73$).

DISCUSSION

The number of different choice situations an individual faces is likely too vast for an optimal decision to evolve for each one (Hutchinson & Gigerenzer, 2005; McNamara & Houston, 2009; Fawcett et al., 2013). Therefore, individuals may need to resort to comparative, rather than absolute, decisions (Bateson & Healy, 2005). Indeed, both human consumers and non-human animals are known to employ such decision mechanisms, sometimes resulting in choices that depend on the range of available options or are in other respects irrational (Tversky & Simonson, 1993; Highhouse, 1996; Bateson et al., 2003). Accordingly, we tested whether sand goby males might be affected by the number and type of choices when choosing a nesting resource. We found no differences in sand goby males' nesting resource choice between our binary (two options) and ternary (third option also available) choice scenarios. Hence, sand gobies have nesting resource size preferences that are independent of the number of options available for comparison.

In most of our treatments (arched: S vs. M and S vs. L; flat: all treatments; Figure 3), male sand gobies chose the larger of the offered nesting resources. Similarly, previous studies have shown that the size of nesting resources, or completed nests, is a relevant consideration for many species in terms of the number of eggs that fit in the nest (Snow, 1978; Lindström, 1988), mate attraction (Hastings, 1988; Takahashi & Kohda, 2002; Lehtonen et al., 2007; Pärssinen, Kalb, Vallon, Anther, & Heubel, 2019), egg/offspring care (Lindstrom & Hellström, 1993; Hoi, Schleicher, & Valera, 1994), susceptibility to nest take-overs or parasitic fertilisation attempts (Lindström & Pampoulie, 2005; Tibbetts & Shorter, 2009), and predation risk (Møller, 1990; Lindström & Ranta, 1992; Biancucci & Martin, 2010). The preferences were also sensitive to nesting resource architecture, suggesting that resource architecture is an important factor for nest builders, and should be considered by researchers studying nesting behaviour. Indeed, besides resource size, other nesting resource characteristics, or characteristics of the site of nesting (Barea & Watson, 2013), are likely to impact offspring success. In the current study, the M (medium-sized) option was more popular than L (large) when both options were arched, whereas the preference order was the opposite for flat nesting resources (Figure 3). More generally, the relative popularity of the L option was lower when the available nesting resources were arched, compared to when the resources were flat.

We consider two mutually non-exclusive, ecologically relevant explanations for the result. First, arched resources are similar to empty mussel shells that many marine gobies, including sand gobies, commonly use as nesting resources. Large arched resources, however, are outside the size range of mussel shells gobies encounter in the study area (northern Baltic Sea), whereas this population of gobies commonly uses flat stones of large surface area for nesting (Lehtonen & Lindström, 2004; Wong et al., 2008). Second, when a nesting resource is smaller, the arched shape may allow a fast initiation of nest-building with a low energy expenditure, whereas the higher arc of a larger resource may be linked to increased costs of nest building, maintenance or defence. More generally, the arched shape may amplify the maintenance and guarding costs associated with occupying a larger resource. However, further research is needed to test these possibilities (see also Lehtonen & Wong, 2020).

The cost-benefit ratio related to a specific resource may also depend on the body size of the nest builder. For example, larger males may be able to cope better with the demands of maintaining and defending nests built using larger nesting resources. Indeed, we found that larger males chose larger nesting resources. This result is consistent with previous studies showing that larger individuals use larger nesting resources or build larger nests in a number of taxa (Lee & Peng, 1981; Takegaki, Matsumoto, Tawa, Miyano, & Natsukari, 2008; Deeming, 2013; Carriço, Amorim, & Fonseca, 2014), including sand gobies (Kvarnemo, 1995; Björk & Kvarnemo, 2012; Japoshvili et al., 2012; Lehtonen et al., 2016). In contrast, body condition did not have a significant effect on resource choice. This finding probably indicates that the returns from obtaining a nesting resource of a certain size are linked much more tightly to body size than body condition. Males of species with paternal egg care (Manica, 2002; Deal & Wong, 2016), including sand gobies (Lissåker, Kvarnemo, & Svensson, 2003; Klug, Lindström, & St Mary, 2006; Deal, Lehtonen, Lindström, & Wong, 2017), have the option of improving their body condition later by cannibalising eggs, once some have already been laid in the nest. Such filial cannibalism provides opportunities for rapid improvement of energy reserves, which may decouple a male's pre-nesting body condition from his (optimal) nesting resource choice. It is also conceivable that, by using males that had already started to build a nest in the field, we excluded individuals whose body condition was too low for a nesting attempt. Males below such a threshold may postpone nest building–and hence nesting resource choice–until they have reached a more adequate state of body condition. Therefore, body condition may not be as important in determining nest building behaviours (including resource choice) as some other factors, such as body size, resource size, physiological properties of the environment (Hilton, Hansell, Ruxton, Reid, & Monaghan, 2004; Rushbrook, Head, Katsiadaki, & Barber, 2010; Mainwaring et al., 2012) or predation risk (Candolin & Voigt, 1998; Jones & Reynolds, 1999).

We hypothesised that the differences in the results of previous studies, with regard to nesting resource size preferences (large size the preferred option: Wong et al., 2008; Lehtonen et al., 2013; Flink & Svensson, 2015; medium size preferred: Kvarnemo, 1995; Japoshvili et al., 2012; Lehtonen et al., 2016), could be due to the different range of options (particularly binary versus ternary) offered in those studies. However, our results suggest that a more important factor differing between these studies is probably nesting resource architecture. In particular, we found that choices of sand goby males did not differ in relation to the number of different options, whereas nesting resource architecture did impact the choice, even when the area available for eggs was kept constant. In accordance with the current results, earlier studies that showed a preference for medium-sized nesting resources typically not only offered three options instead of two, but also used the arched nesting resource type (e.g. Kvarnemo, 1995; Japoshvili et al., 2012; Lehtonen et al., 2016), whereas studies that showed a preference for the largest available option tended not only to lack medium-sized option but also to use flat nesting resources (e.g. Lindström, 1988; Wong et al., 2008; Lehtonen et al., 2013; Flink & Svensson, 2015). Therefore, the different findings of the previous studies are better explained by resource architecture than the number of options that were offered. Sand gobies seem to make absolute rather than relative resource choices.

To conclude, the results show that nesting resource size, nest builder's own body size and resource architecture are all important in determining male choice of nesting resources. In contrast, the choices were robust with regard to the range of available choice options and male body condition. Taken together, such results underscore the value of disentangling the roles of intrinsic and extrinsic factors in influencing individual behavioural decisions over resource choice and nesting behaviour.

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Figure captions

Figure 1

Schematic presentation of the two nesting resource architecture types, arched and flat. The lower part of the figure shows the three different sizes used in the laboratory experiments (not to scale).

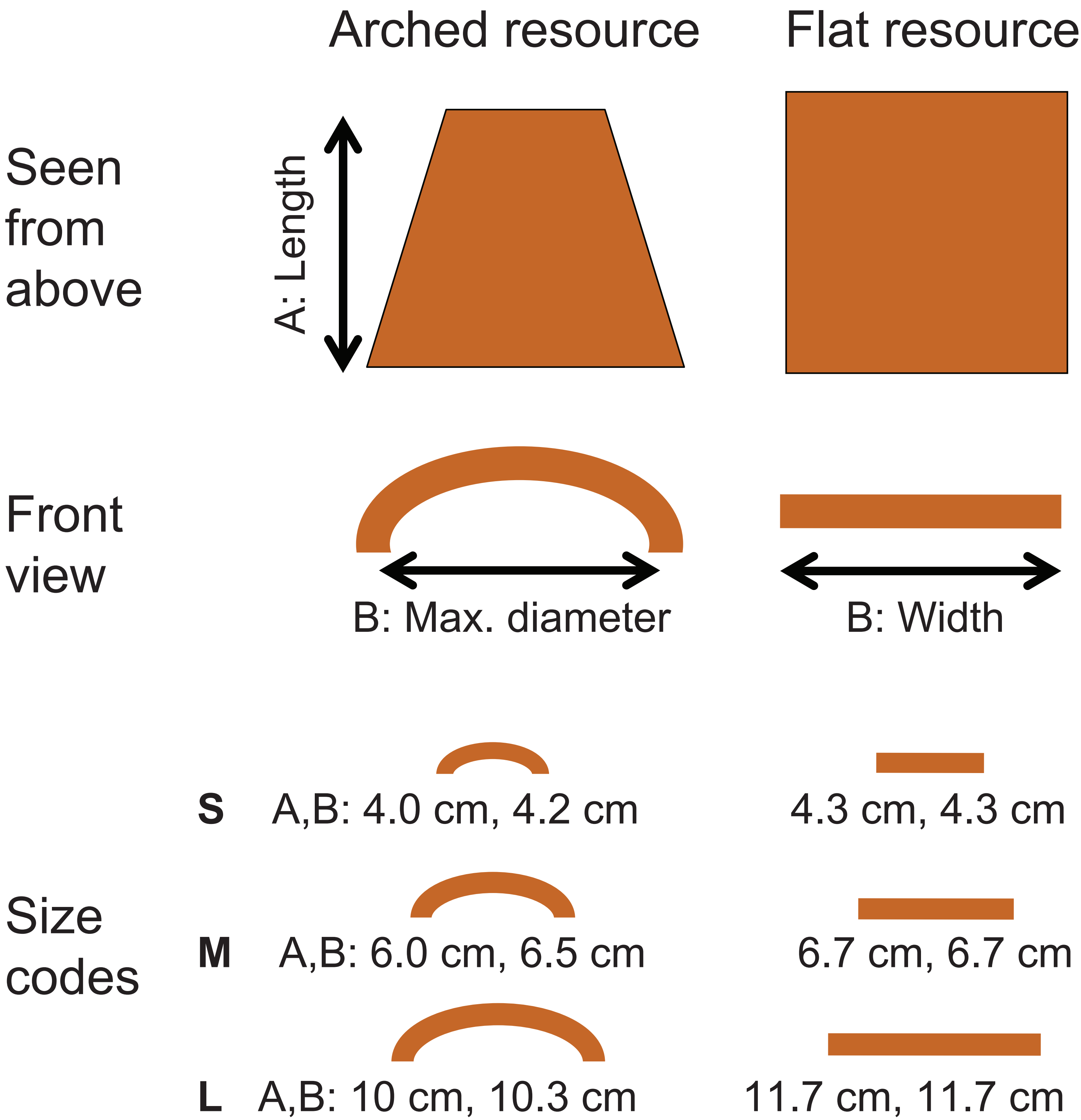
Figure 2

Comparison of relative nesting resource size choices of male sand gobies when two focal size options were offered (binary choice) and when, besides these two options, a third alternative (denoted in parenthesis in the text panel, not shown in the proportion bars) was also available (ternary choice). (a) Sand goby male next to a nest he has built using an arched resource. The comparisons were (b) small vs. medium, (c) medium vs. large and (d) small vs. large. Sample sizes for the replicates in which one or the other focal size was chosen are shown.

Figure 3

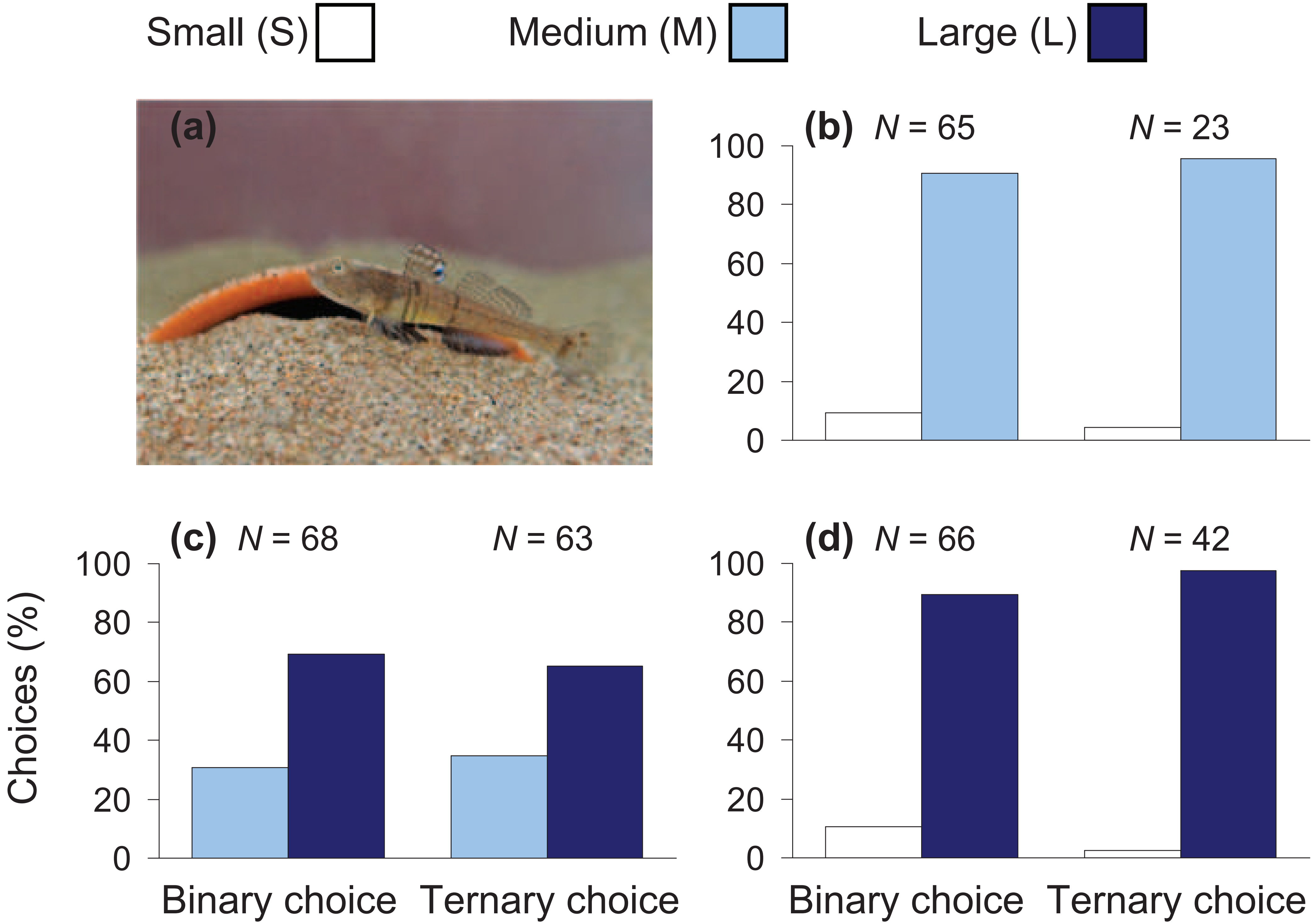
Nesting resource size choices of male sand gobies when the following resource size options were offered: (a) small vs. medium, (b) medium vs. large, (c) small vs. large and (d) small vs. medium vs. large. The offered resources were of either arched or flat architecture, with the figure showing how the resource size choices differed under these two conditions. Sample sizes (the numbers of choices) are also shown.

Figure 1



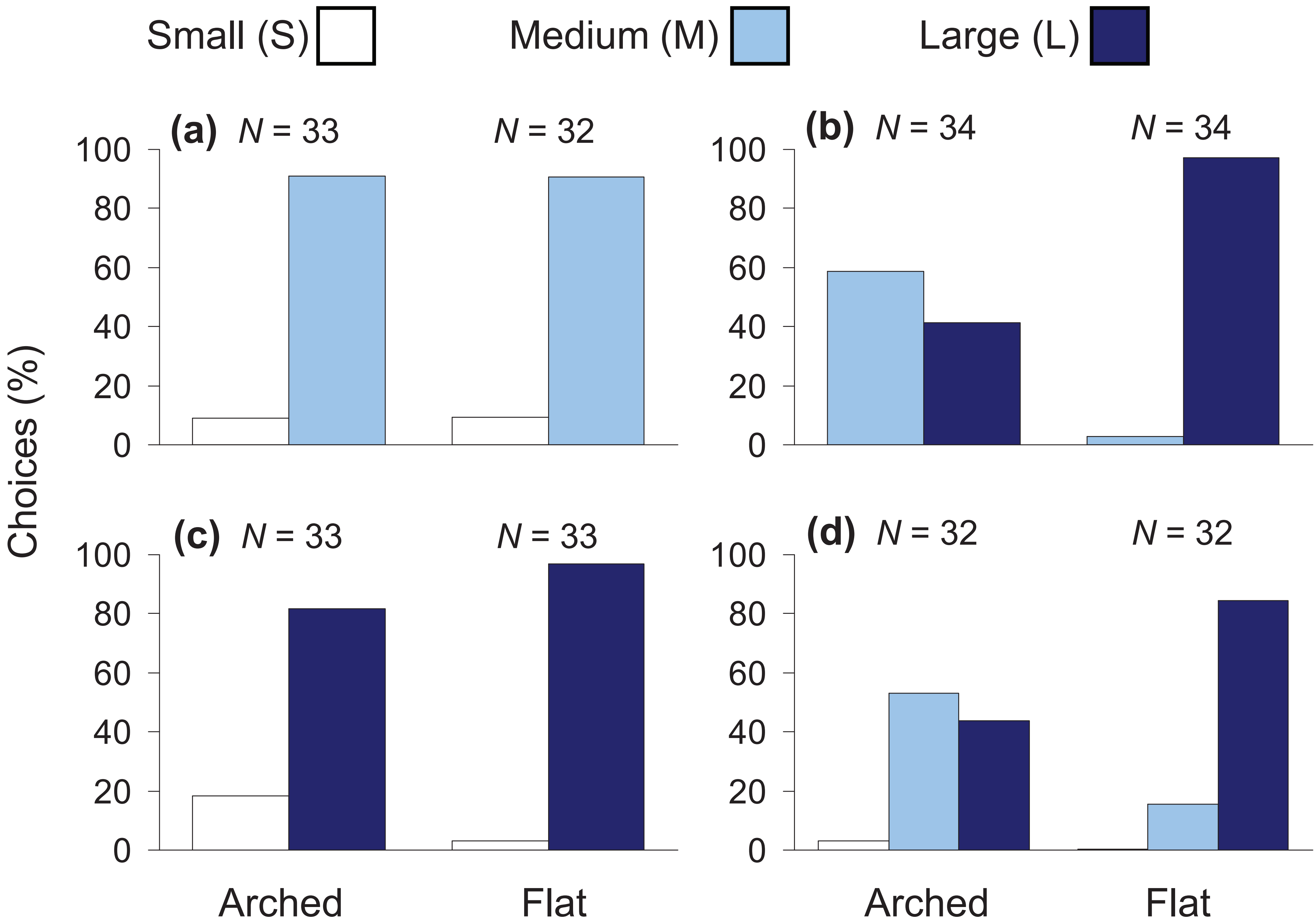
Arched resource
Flat resource
Seen from above
A: Length
Front view
B: Max. diameter
B: Width
Size codes
S A,B: 4.0 cm, 4.2 cm
4.3 cm, 4.3 cm
M A,B: 6.0 cm, 6.5 cm
6.7 cm, 6.7 cm
L A,B: 10 cm, 10.3 cm
11.7 cm, 11.7 cm

Figure 2



Small (S)
Medium (M)
Large (L)
(a)
(b) N = 65
N = 23
(c) N = 68
N = 63
(d) N = 66
N = 42
Choices (%)
100
80
60
40
20
0
Binary choice
Ternary choice

Figure 3



Small (S)
Medium (M)
Large (L)
Choices (%)
(a) N = 33
N = 32
(b) N = 34
N = 34
(c) N = 33
N = 33
(d) N = 32
N = 32
100
80
60
40
20
0
Arched
Flat
Arched
Flat