

Facultative adjustment of pre-fledging mass loss by nestling swifts preparing for flight

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Nestling birds often maintain nutritional reserves to ensure continual growth during interruptions in parental provisioning. However, mass-dependent flight costs require the loss of excess mass before fledging. Here we test whether individual variable mass loss prior to fledging is controlled through facultative adjustments by nestlings, or whether it reflects physiologically inflexible developmental schedules. We show that in the face of natural and experimental variation in nestling body mass and wing length, swifts always achieve very similar wing loadings (body mass per wing area) prior to fledging, presumably because this represents the optimum for flight. Experimental weights (approx. 5% body mass) temporarily attached to nestlings caused additional reductions in mass, such that final wing loadings still matched those of control siblings. Experimental reductions in nestling wing length (approx. 5% trimmed from feather tips) resulted in similar additional mass reductions, allowing wing loadings at fledging to approach control levels. We suggest that nestlings may assess their body mass relative to wing area via wing flapping and special 'push-ups' (on the tips of extended wings) performed in the nest. Thus, by facultatively adjusting body mass, but not wing growth, nestling swifts are always able to fledge with aerodynamically appropriate wing loadings.

Keywords: body mass; wing length; mass-dependent flight costs; aerodynamics; common swift; *Apus apus*

1. INTRODUCTION

Nestling birds commonly face the problem of unpredictable parental provisioning schedules due to, for example, variation in weather conditions that may affect food availability (Lack 1953; Ricklefs & Schew 1994; Gray & Hamer 2001). Nestlings may therefore store nutrients as insurance to maintain maximal growth, even during poor feeding conditions (Lack 1953; Ricklefs 1968; Hudson 1979; Philips & Hamer 1999). Upon fledging, however, birds experience mass-dependent flight costs, either because of the energetic cost of carrying excess weight or the increased risk of predation due to being less manoeuvrable (Witter & Cuthill 1993). As a consequence, the optimum level of body reserves (e.g. mass of fat) that a young bird should carry drops dramatically at fledging, and rapid pre-fledging mass recession is necessary to change from a fat immobile nestling to a slim and efficient flying juvenile (Martins 1997; Mauck & Ricklefs 2005). Such physiological and behavioural trade-offs prior to fledging are therefore interesting, because they shed light upon the nature of adaptive growth and development schedules in the life history of young birds, as well as inform us about aerodynamic demands and physical adaptations for flight in birds.

Pre-fledging mass recession is most pronounced in seabirds, and most research in this area has therefore been carried out on nestling growth and parental provisioning in these species (e.g. Gray & Hamer 2001; Philips & Hamer 1999; Mauck & Ricklefs 2005). However, pre-fledging mass loss also occurs in aerial insectivores,

especially in the common swift (*Apus apus*), probably because parental foraging is particularly influenced by occasional bad weather in these species (Lack 1956; Martins & Wright 1994). Swifts also provide little or no post-fledging care, and so young birds have to be ready to fly and fend for themselves immediately upon leaving the nest (Lack 1956). Fledgling swifts are unable to return to the nest, and these birds spend most of their lives on the wing, so young swifts usually do not land until they themselves nest in future breeding seasons (Lack 1956). It is therefore critical that at the end of the period of growth and development in the nest all fledglings have an aerodynamically efficient body shape for immediate flight (i.e. the appropriate 'wing loading' (body mass per wing area)). As might be expected, well-fed, heavier nestlings raised in smaller broods and under more favourable weather conditions, tend to lose more mass (i.e. fat and/or other nutrient reserves) before they fledge (Martins 1997). This is not simply the result of parents imposing forced reductions in feeding rates prior to fledging, but appears to be a consequence of individual nestlings modifying their begging behaviour (and so food consumption) with the purpose of their bodies meeting the aerodynamic requirements for flight (Martins 1997).

Given the considerable natural variation that exists in body mass and wing length in nestling swifts (i.e. up to 30%; Martins 1997), how do individuals assess how much mass they need to lose in order to optimize future aerodynamic performance? Is pre-fledging mass recession physiologically pre-programmed to match each nestling's body size (the 'inflexible growth schedule' hypothesis), or can individual nestlings assess changes in their body mass

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and wing length and facultatively adjust their personal rate of mass loss (the 'facultative adjustment' hypothesis)? To address these two hypotheses, we experimentally increased nestling body mass for two weeks prior to fledging by temporarily attaching a small lead weight, representing approximately 5% extra body mass, to the feathers in the centre of the back. In a second experimental group, we trimmed the primary wing feathers, representing approximately 5% reduction in wing length, two weeks prior to fledging. We then compared the final body mass, wing length and wing loading values of these two experimental groups with their unmanipulated (control) siblings in the same nests. The facultative adjustment hypothesis predicts additional pre-fledging body mass loss and/or increased wing growth in both groups of experimentally manipulated nestlings. In this way, wing loading values in experimentally manipulated nestlings will be facultatively adjusted in order to match those of control nestlings. In contrast, the inflexible growth schedule hypothesis predicts no such adjustments in the later stages of nestling development in response to our manipulations. In this case, we might expect inappropriately large final wing loadings in the two manipulation groups as compared to their control nest-mates. This experimental manipulation, carried out on nestlings in two different brood sizes, therefore provides a critical test for the existence of facultative control of pre-fledging growth and development in accordance with the aerodynamic requirements for flight.

2. MATERIAL AND METHODS

(a) *The study population*

Adult swift body mass during provisioning varies between 36 and 46 g (Martins & Wright 1993a); however, two weeks prior to fledging (i.e. 31 days), nestlings may actually be heavier than their parents (i.e. range 35–60 g; Martins 1997). They then sharply lose up to 20% of their body mass prior to fledging in order to approach adult weights when they leave the nest (Martins 1997).

The study site was The University Museum tower at Oxford. Fieldwork was carried out during June–August 2000–2002. This well-established nest-box colony has been the site of previous work on the breeding biology of swifts by David Lack (Lack 1956) and Thais Martins (Martins & Wright 1993a,b, 1994; Martins 1997).

(b) *Experimental design*

The experimental manipulation of 'weighted' nestlings involved a 2 g lead weight strip (approx. 5% body mass) attached using superglue to body feathers in the middle of the back (i.e. the nestling's centre of gravity) at 31 days of age (i.e. prior to the majority of any pre-fledging mass loss; Martins 1997). This weight was removed by cutting off the tips of the body feathers a day or two before fledging at 42–44 days. The experimental reduction of wing length in 'trimmed' nestlings (also at 31 days) was obviously not reversible, and so were very carefully trimmed with a scalpel only 10 mm from the tips of the primary feathers (approx. 5% wing length), as measured along a straightened wing. This feather cut was carried out with the wing extended in the normal flight position, and at an angle greater than 90° from the leading edge of the wing, designed so as to maintain a natural shape to the tip of the wing.

In six broods of two, one of the nestlings was randomly assigned to the experimental weighted treatment, while its sibling acted as an unmanipulated 'control'. Likewise, in another six broods of two, one randomly chosen nestling was experimentally trimmed and its sibling acted as a control. This resulted in 12 control nestlings, plus six weighted and six trimmed nestlings from the 12 broods of two in the experiment. In addition, in eight broods of three, each of the three treatment groups could be represented within each brood. Therefore, in each brood of three, one randomly assigned nestling was weighted, one was trimmed and the third one acted as the control. This resulted in eight nestlings in each of the three treatment groups from the eight broods of three in the experiment. The single unmanipulated nestling in each of these 20 nests (12 broods of two plus 8 broods of three) represented a control in that it experienced identical conditions in the nest as the manipulated nestlings, and the same general levels of handling and disturbance. To further equalize nestling experiences during the manipulation period, these control nestlings were also removed from the nest at 31 days and put through a 'sham' experimental treatment (i.e. the control siblings of all trimmed nestling were touched with the scalpel on their wing tips, and the control siblings of all weighted nestlings were repeatedly touched in the middle of their back as in the gluing process).

Due to possible welfare concerns, we kept sample sizes to a minimum and exploited the within-brood experimental design that provided standardized comparisons between manipulated and unmanipulated nestlings within the same broods. All procedures and experimental manipulations were carried out under UK Home Office and English Nature licences. To the best of our knowledge, all manipulated and control nestlings fledged normally at the age expected, and with no adverse short-term or long-term consequences.

(c) *Data collection*

Daily measurements were taken of nestling body mass using an electronic balance (to the nearest 0.1 g) and wing length using a wing rule (to the nearest millimetre). Calculations of wing loading followed previous methods (Pennycuik 1989; Martins 1997), where wing area approximates to twice the sum of the area of a rectangle (as described by the ulna, radius, humerus and secondaries) plus the area of a triangle (as described by the wing length, carpometacarpus and primaries).

(d) *Statistical analysis*

Given the inclusion of broods of two and three in this experimental design, nestlings in the two manipulation groups (weighted and trimmed) had to be compared against two different, but overlapping, subsets of control nestlings. In this way, each manipulated nestling could always be statistically compared against its own control sibling that it shared the nest with. Therefore, data from the two manipulation groups were analysed separately each time in two different paired *t*-tests, each against their own subset of controls (i.e. weighted versus control A, and then trimmed versus control B). The effect of brood size (i.e. 2 versus 3 nestlings) was tested using unpaired *t*-tests, based upon a mean value per nest, which included all nestlings (manipulated and control). The interaction term effect of brood size with experimental treatment also had to be analysed separately. This was done by first calculating the mean experimental effect (i.e. the difference between manipulation

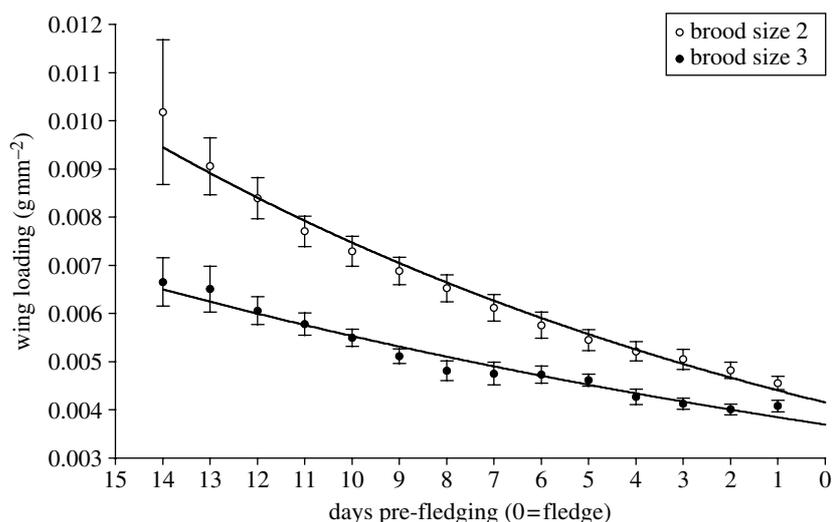


Figure 1. Convergence of wing loading values (mean \pm s.e. body mass per wing area) during the last two weeks prior to fledging (at day=0) for unmanipulated control nestling swifts from broods of two ($n=12$) and three ($n=8$). Best-fit lines are shown for exponential declines in mean wing loading values (broods of two, $r^2=0.967$, $n=14$, $p<0.001$, $y=0.0037 e^{-0.0404x}$; broods of three, $r^2=0.985$, $n=14$, $p<0.001$, $y=0.0042 e^{-0.0588x}$).

and control nestling values) per brood and then comparing these values for the two different brood sizes in unpaired t -tests. All data conformed to assumptions of normality and equality of variances (unless otherwise stated), and therefore all tests were parametric. Results are presented as mean \pm s.e., with two tailed p -values being used throughout.

3. RESULTS

(a) Natural variation due to brood size

Control nestlings were heavier in broods of two, and therefore reduced their pre-fledging wing loading (body mass per wing area) at a much greater rate than the lighter control nestlings in broods of three (figure 1; $t_{18}=3.265$, $p=0.009$). This occurred mostly because control nestlings in broods of two lost significantly more mass between age 31 days and fledging as compared with control nestlings in broods of three ($t_{18}=5.766$, $p<0.001$), since rates of wing growth did not differ between brood sizes during the same period ($t_{18}=0.152$, $p=0.883$).

(b) Experimental effects on body mass

Weighted nestlings lost significantly more mass in the two weeks before fledging as compared with control nestlings (figure 2a; paired $t_{13}=4.695$, $p<0.001$), as predicted by the facultative adjustment hypothesis. The scale of this additional mass loss by weighted nestlings neatly matched the size of the experimental 2 g extra mass they were given (figure 2a). Trimmed nestlings also lost significantly more mass than controls (paired $t_{13}=9.059$, $p<0.001$), again as predicted by the facultative adjustment hypothesis. Interestingly, this effect was similar in scale to that of weighted nestlings (figure 2a), suggesting that an approximately 5% manipulation of wing length approximates to an approximately 5% manipulation of body mass in this system. As expected from the analyses (§3a) of control nestlings in figure 1, the mean level of pre-fledging mass loss across all nestlings in the experiment was significantly greater for broods of two compared to broods of three (figure 2a; $t_{18}=3.941$, $p=0.001$), but the size of the experimental effects on mass loss did not differ between brood sizes ($t_{18}=0.696$, $p=0.495$).

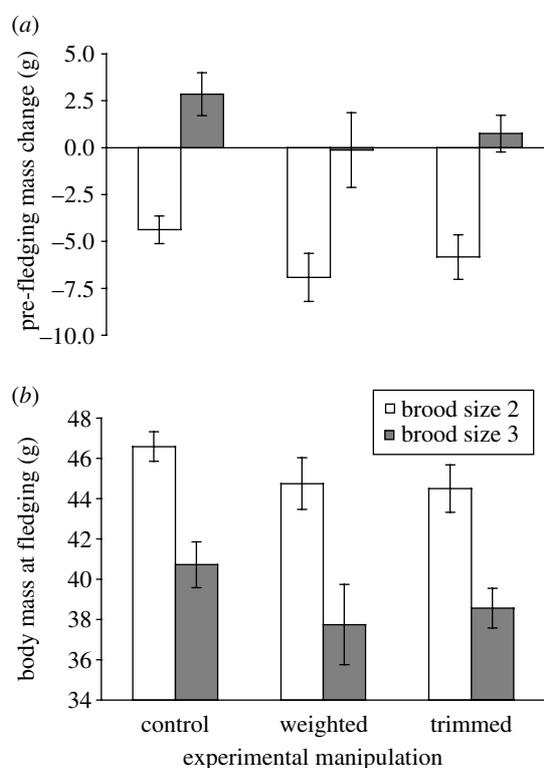


Figure 2. The effect of within-brood experimental manipulations, involving the addition of 2 g (approx. 5%) to body mass of 'weighted' nestlings, and the reduction by 10 mm (approx. 5%) of wing length in 'trimmed' nestlings, as compared to their unmanipulated 'control' siblings, in brood sizes of 2 and 3, for: (a) pre-fledging mass change (between 31 and 44 days of age); (b) final body mass at fledging.

As a consequence of these differences in mass loss, there were significant differences in body mass at fledging, with both manipulation groups fledging at significantly lighter weights than controls (figure 2b; control versus weighted nestlings, paired $t_{13}=2.553$, $p=0.024$; control versus trimmed nestlings, paired $t_{13}=4.553$, $p=0.001$). If the (now removed) experimental weights were to be included in these final body mass calculations, weighted nestlings would actually have fledged at similar mass to

control nestlings (paired $t_{13}=0.554$, $p=0.589$). As expected, nestlings in all three experimental groups raised in broods of two fledged at significantly greater body mass compared with nestlings in broods of three (figure 2b; $t_{18}=8.498$, $p<0.001$), but the size of the experimental effects on final body mass did not differ between brood sizes ($t_{18}=0.222$, $p=0.827$).

(c) *Experimental effects on wing length*

The differences in wing growth during the last two weeks before fledging were less obvious than the changes in body mass. Weighted nestlings appeared to grow their wings at a slightly lower rate compared with their controls (weighted 30.86 ± 3.13 mm versus control 35.36 ± 3.42 mm: paired $t_{13}=2.716$, $p=0.018$). The cause of this result is unclear, because it seems to have been a consequence of a combination of faster than expected wing growth by the control siblings and slower than expected wing growth by weighted nestlings. This is further highlighted by the fact that wing growth did not differ between trimmed and control nestlings (trimmed 32.64 ± 3.27 versus control 33.36 ± 3.63 mm: paired $t_{13}=0.212$, $p=0.836$), with the mean values in both these cases falling neatly between the mean values for weighted nestlings and their control group (above). There were no significant differences in wing growth between brood sizes (two chicks 66.00 ± 4.14 versus three chicks 98.25 ± 14.65 : t -test for unequal variances $t_{8,13}=2.119$, $p=0.066$). Again, brood size did not interact with the effects of the experimental treatments ($t_{18}=0.697$, $p=0.495$).

These possibly minor random differences in wing growth rates did not seem to affect the end result, because weighted and their control nestlings fledged with similar wing lengths (weighted 163.29 ± 2.76 mm versus control 164.57 ± 1.21 mm: paired $t_{13}=0.457$, $p=0.655$). Trimmed nestlings obviously fledged with significantly shorter wings as compared with their controls (trimmed 157.71 ± 1.57 mm versus control 166.64 ± 0.91 mm: paired $t_{13}=7.373$, $p<0.001$). However, if the removed 5% wing lengths were to be added to each nestling in the trimmed group, there was then no significant difference in wing lengths at fledging between trimmed and control nestlings (untrimmed 168.21 ± 1.32 mm versus control 166.64 ± 0.91 mm: paired $t_{13}=1.479$, $p=0.163$).

(d) *Experimental effects on wing loading*

As predicted by the facultative adjustment hypothesis, weighted nestlings compensated for the addition of the extra experimental mass and slimmed down at an accelerated rate in order to reduce their wing loading to a level similar to that of control nestlings (weighted 4.3 ± 1.0 mg mm⁻² versus control 4.4 ± 1.5 mg mm⁻²: paired $t_{13}=0.087$, $p=0.932$). Nestlings with trimmed wings also showed a similar level of experimentally induced increase in their rate of pre-fledging mass loss, but this may not have been sufficient, because they still fledged with a greater wing loading than their controls (trimmed 4.5 ± 1.3 mg mm⁻² versus control 4.2 ± 0.9 mg mm⁻²: paired $t_{13}=3.680$, $p=0.003$). However, this significant difference may be more due to an unexplained reduction in the mean control nestling wing loadings in this case, rather than any excess in trimmed nestling wing loadings (i.e. note the intermediate values for weighted nestlings and their controls above).

4. DISCUSSION

As might be expected from previous work on this system (Lack 1956; Martins 1997), heavier nestlings raised in broods of two in 2000–2002 lost significantly more mass than nestlings in broods of three during the last two weeks prior to fledging. However, the most interesting feature of this result (shown in figure 1) is the way in which wing loadings for nestlings in the two brood sizes converged close to the day of fledging. Unfortunately, we were unable to collect the data needed to test definitively if the nestlings from these two different brood sizes still differed at the moment of their first flight. It is possible that the two brood sizes converged on precisely the same wing loading at fledging. But it is also possible that larger nestlings from broods of two fledged with slightly greater wing loadings: perhaps because their better nutrition and muscle development allowed them to adopt a more powerful and heavier body type. Nevertheless, despite their very different body sizes prior to the period of mass recession, all nestlings appeared to fledge at a more or less similar wing loading, presumably because this is the best one for flight in young swifts (Martins 1997).

This convergence towards a common wing loading value was also apparent following the experimental treatments. Weighted nestlings seemed to detect the addition of the experimental mass and facultatively increased their rate of pre-fledging mass recession in order to still fledge with wing loadings similar to that of their unmanipulated control siblings. This same response was apparent in the experimental nestlings with trimmed wings, but with a slightly less convincing end result. Trimmed nestlings clearly detected the manipulation, and did increase their rate of pre-fledging mass loss in response, but perhaps not quite sufficiently. So, although the manipulation effect was in the predicted direction, trimmed individuals fledged with slightly greater wing loadings as compared with their particular unmanipulated control siblings. Swift nestlings were possibly less able to respond to the experimental manipulation of wing length, as compared with their experimental response to manipulations of body mass. One reason for this might be that, by trimming the wings in this way, we did not accurately represent natural allometric changes in wing shape/size. Thus, trimmed nestlings may have made slightly incorrect assessments regarding our experimental changes to their wing loadings, presumably in a way that does not occur in response to natural variation in wing length. However, much of this remains speculation until we know more about the proximate mechanism used by nestling swifts to make these adjustments (see below). An improved manipulation of nestling wing length would also require greater knowledge about the exact shape of the growing swift wing, especially the wing tip, and how this affects fledgling flight performance.

The main result presented here is that nestling swifts do have the ability to make individual facultative adjustments in their pre-fledging mass loss, and are not tied to an inflexible developmental schedule. This apparently adaptive flexible response is seemed to be achieved by nestlings simply limiting their food intake during the last two weeks before fledging. This occurred through an obvious reduction in individual nestling begging effort and the subsequent reduction in the rate of food delivery by their parents (S. Markman & S. M. Denney 2000–2002,

personal observation; and see Martins 1997). It is possible that our weighted nestlings lost more mass prior to fledging because they experienced greater energetic demands in the nest as a result of carrying around the experimental mass. However, given the range of movement by these birds in the nest (see below) this seems unlikely to have been a sizeable effect. The similar level of mass loss by individuals in the trimmed experiment group also clearly argues against this as an explanation for our results here. Therefore, during the last two weeks in the nest, nestling swifts appear to voluntarily lower their food intake and individually reduce their body mass (but interestingly not increasing their wing growth) in order to achieve the appropriate wing loading for flight.

The facultative control of pre-fledging mass loss must have evolved for individual nestlings to cope with natural stochastic variation in their body mass and wing length. Indeed, adverse effects of unpredictable weather mean that developmental plasticity is especially prevalent in the growth schedules of nestling swifts (Lack 1956; Martins 1997; Bize *et al.* 2003), as compared with other species of birds, which show less flexible schedules of nestling growth (Ricklefs 1979; Metcalfe & Monaghan 2001) and fledging (Lemel 1989; Nilsson & Svensson 1996). Inflexible pre-fledging mass recession has generally been associated with water loss as a result of the integument drying out (Ricklefs 1968; O'Connor 1977; Bryant & Gardiner 1979). In contrast, the individually flexible rates of mass loss demonstrated here suggest that it must be largely lipid reserves that are being lost prior to fledging by nestling swifts (see also Martins 1997). Therefore, it seems to be the fat stores used as insurance during the early nestling period that are being adaptively shed before fledging in these systems.

The question now is: how do nestling swifts assess their body mass and wing length, even after artificial manipulation? Like most nestling birds, swifts only have enough room in their nest cavities to flap their wings during the latter stages of the nestling period. This normally involves 22–150 s bouts, where nestlings rapidly move their wings up and down in short bursts just like adult swifts in flight (S. M. Denney 2002, personal observation via the glass-backed nest-boxes in the Museum tower). This behaviour may have some function in exercising or stretching the flight muscles (see Teather 1993). However, unlike seabirds, swifts cannot make small test-flight hovers or excursions and still return to their nests. Therefore, this repeated wing flapping behaviour may also allow nestlings to assess wing size, because wing area must be proportional to the effort it takes to flap a wing against air resistance. Wing flapping may even provide a direct measure of wing loading, as nestlings are sometimes able to take their feet off the ground for a few seconds, but only a day or two before fledging and when a sharp breeze enters the nest cavity. Even more interestingly, swift nestlings also perform 'push-ups' in the nest (Lack 1956), in which they extend their wings and lift their bodies clear of the floor for 2–9 s. This unusual behaviour also seems unlikely to have evolved solely for the purpose of exercise, especially when used in conjunction with wing flapping. It is possible that it allows the adaptive adjustment of flight muscle mass growth according to the predicted demands of flight. However, we concur with Martins (1997), and suggest that these physical

movements seem most likely to provide these nestlings with a very good way to assess their body mass relative to their wing length.

Nestling swifts may somehow integrate information concerning wing area from flapping with relative body mass from the effort needed to perform push-ups, in order to obtain an accurate estimate of wing loading. This combination of behaviours currently provides the most plausible explanation of how nestling swifts are able to make the necessary adaptive adjustments in their individual rates of pre-fledging mass loss. Such a mechanism of facultative assessment would also explain how they were able to detect and respond to our experimental manipulations of body mass and wing length in order to nevertheless achieve an appropriate wing loading upon fledging. We therefore conclude that our experimental results support the facultative adjustment hypothesis, and that nestling swifts are capable of more than simple inflexible growth schedules in the latter stages of growth and development prior to fledging.

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