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Differential food allocation by male and female great tit, *Parus major*, parents: are parents or offspring in control?

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The distribution of food among altricial bird nestlings is the result of an interaction between parental feeding decisions and scramble competition between nestmates. Both young and parents can potentially be in control of the outcome of this interaction. In great tits, each parent feeds from a fixed location on the nest rim, thereby forcing nestlings to choose between the father's and the mother's location. It was previously found that hungry nestlings approached the female preferentially and were more likely to be fed, appearing as if females showed a stronger preference to feed hungry young than males. However, nestlings were free to move in that study, and the effects of nestling positioning could not be disentangled from those of parental food allocation decisions. Here, we experimentally divided broods into two halves and randomly assigned each half of the brood to one side of the nest cup where only one parent could feed them. One nestling in each half-brood was food deprived to manipulate short-term hunger state. Both parents showed a similar preference to feed the more hungry nestlings, suggesting that the previously observed difference was due to offspring positioning rather than active parental choice. Our study shows that food allocation is partially under nestling control and suggests that nestlings adjust positioning and begging behaviour to the profitability of a given position in the nest cup.

Keywords: begging behaviour; food allocation; great tit; parental care; parent–offspring conflict; *Parus major*; scramble competition

In altricial birds, where offspring are highly dependent on parental food provisioning for their growth and survival, different members of a family can be in conflict over the amount or distribution of parental care and resources (Trivers 1974). Nestlings are expected to try to secure more care from a provisioning parent than is in the interest of the parent to give because the optimal level of care is not equal for parent and offspring (Mock & Parker 1997). Moreover, in species with biparental care there could also be diverging interests between mothers and fathers over parental care and its distribution among siblings (Houston & Davies 1985; Parker 1985) because males and females may differ in their reproductive constraints and in their trade-off between parental care and other activities.

Brood division between parents caring for young birds, defined as preferential food provisioning for different subsets of their brood by the two caring parents, is common at the fledgling stage (Byle 1990; Lessells 2002; Leedman & Magrath 2003). After fledging brood division can be spatially achieved in that particular nestlings follow, associate with and get fed by one of the two parents. More cryptic brood division could also occur inside the nest cup of altricial birds with biparental care (Slagsvold 1997). Both inside the nest of several species (Bengtsson & Rydén 1981; Stamps et al. 1985; Gottlander 1987; Leonard & Horn 1996; Krebs et al. 1999) and after fledging (Slagsvold et al. 1994), fathers tend to preferentially feed larger offspring, whereas females tend to favour small offspring (Lessells 2002), although other patterns also occur (Harper 1985; Smiseth et al. 1998; Wheelwright et al. 2003; Whittingham et al. 2003). There are different ways by which such feeding outcomes may be mediated. First, there could be direct assessment of offspring phenotype by the parents and different active preferences by

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females and males with respect to nestling phenotype. Second, nestlings of different phenotype may differ in their capability to beg. If mothers and fathers show different sensitivities to begging, differential feeding by the two parents with respect to nestling phenotype may ensue. In several species, males are indeed more responsive to begging intensity than females (Stamps et al. 1985; Sasvári 1990). Conversely, females are thought to evaluate other phenotypic characteristics of the nestlings more than males, in particular size (Stamps et al. 1985), and modulate their response to begging based on such information. Finally, because the relative positioning of nestlings on the small spatial scale of a nest cup influences feeding outcomes (McRae et al. 1993; Leonard & Horn 1996; Ostreiher 2001), partial brood division where males and females feed different nestlings preferentially might occur within nests if mothers and fathers use different locations from which they feed (Slagsvold 1997). Food distribution among nestlings is thus the result of a behavioural interaction between sibling competition, that is, nestmates' positioning and begging behaviour, and parental feeding decisions.

In the great tit, each parent provisions food from a distinct and temporally stable position on the nest rim consistently throughout the breeding season (Kölliker et al. 1998; Lessells et al. 2006). The nestlings are able to learn their parents' feeding positions, which may lead to scramble competition among nestlings for access to these 'begging patches' (Kölliker & Richner 2004). As experimentally shown (Tanner et al. 2007), parents can reduce the overall level of sibling competition by choosing feeding locations that are farther apart from each other. In addition, food-deprived nestlings were observed to approach their mother's feeding position preferentially and were more likely to be fed by the latter than by their father (Kölliker et al. 1998), suggesting sex-specific food provisioning rules that affect nestling positioning. However, in that study (Kölliker et al. 1998), nestlings were free to choose their positions, and the effects of nestling positioning and parental choice on food distribution were hence confounded. New studies are thus required to investigate the relative importance of nestling and parental control (Slagsvold 1997) on the evolution and maintenance of differential food allocation patterns by mothers and fathers.

The aim of the present experiment was to experimentally separate the effects of nestling positioning behaviour and parental allocation decisions on the distribution of food among nestlings. For this purpose, we divided broods by the use of Plexiglas barriers and thus forced each nestling into a position where it could be fed only by either the male or the female parent. We assessed the consequences on food distribution among nestlings and the effect on change in body mass. In addition, one nestling in each half-brood was food deprived for a short period before the experiment to test whether both parents show a similar preference for feeding hungry nestlings or, as previously found under unconstrained nestling positioning (Kölliker et al. 1998), whether females feed hungry offspring at higher rates than males independent of the effect of nestling positioning. Thus, if food allocation differences between females and males are due to differential nestling positioning but not active parental preferences, we predict, under constrained chick positioning, that food-deprived nestlings should be fed equally by males and females. Alternatively, if the sex difference in food allocation patterns is due to active parental choice, females should feed hungry nestlings more frequently than males. Since it had also been suggested that male nestlings are more competitive than females (Teather 1992; Leech et al. 2006), we additionally assessed the effect of nestling sex on food allocation.

METHODS

This study was conducted in spring 2005 on a population of great tits breeding in nestboxes in the Könizbergwald, a deciduous forest near Bern, Switzerland. Nestboxes were checked regularly from the beginning of April to monitor the start of egg laying, incubation and hatching for each nest. When nestlings were 6 days old, 2–5 μl of blood was taken from their metatarsal vein and kept frozen in ethylenediaminetetraacetate for subsequent molecular sex determination. Nestlings were marked by selectively removing small tufts of downy feathers from their head or wings to make them individually recognizable until they were old enough to be permanently ringed. This is common practice as this down has no known function (hatchlings in other tit species lack some of the tufts). It is very easily removed from the hatchlings without causing any apparent sign of harm. These markings disappear once the head feathers have grown, which is around day 10 after hatching.

Experimental Set-up

On the sixth day after hatching, broods were video recorded for 2 h and 15 min using infrared cameras installed in the upper part of the nestboxes. From these records males and females were identified using the sexual colour dimorphism of the black head cap (dark black: male; greyish black: female) and their specific provisioning sites determined. The position of a parent's head just before feeding was recorded on each feeding event, and the median position was calculated for each parent (Tanner et al. 2007). In the morning of the ninth day after hatching nestlings were ringed with aluminium rings (Station Ornithologique Suisse, Sempach) and ranked in each nest according to their body mass. Pairs were created by grouping two consecutively ranked nestlings. One pair of nestlings was randomly chosen in each nest to be food deprived. They were kept for 2 h in warmed artificial nests under constant observation, whereas their siblings were left in the nest to be normally fed by the parents. The duration of the deprivation period was chosen according to previous studies where no long-term effects were detected (Smith & Montgomerie 1991; Kölliker et al. 1998). Mealworms were available in case starved nestlings showed signs of harm or exhaustion, but this precautionary measure proved unnecessary. After the food deprivation period, all nestlings were returned to their nest. The heaviest nestling of the nest was then randomly assigned to the mother or father side of the nestbox. The entire brood, including the food-deprived nestlings, was divided by alternating male and female side through the mass-ranked list. Because nests could be divided only perpendicularly to the entrance hole, only the nests where one parent landed and fed from the left of the entrance hole and the other one from the right were selected for the brood division experiment. The experiments were carried out on 26 nests each containing 4–10 nestlings (average = 6.8) for a total of 176 nestlings. The experimental brood division appeared to have no harmful effects on nestlings because their body mass after the experiment was not different from the mass of unmanipulated nestlings of the same age ($F_{1,223} = 0.94$, $P = 0.33$). To further support our conclusion of a lack of a long-term effect of the manipulation on body mass, we also calculated the Akaike Information Criterion (AIC) for models with and without the manipulation included (AIC with/without: 1020/1019). Note that AIC is smallest for the best-fitting model (Pinheiro & Bates 2004; Stephens et al. 2007). When a nest contained an odd number of nestlings ($N = 12$), one nestling was brought to another nonexperimental nest containing nestlings of similar age and mass, where it was left for the whole day, and returned to its nest of origin in the evening. Mothers and fathers in a given experimental nest thus each always fed the same number of nestlings. A Plexiglas partition, about 6 cm high, was used to divide the nest into two parts and prevented nestlings from moving to the other side of the nest cup. Parents could not reach nestlings beyond the partition and landed on the intended side of the partition in more than 80% of the visits. Nestlings were marked on their heads with small spots of acrylic paint to make them individually recognizable (Kölliker et al. 1998). The colour used was chosen for its lack of conspicuousness under the dim light inside a nestbox and its contrast with nestling plumage under infrared light on the video recordings. We could thus identify nestlings on the recordings without disturbing parental behaviour. Neither parents nor nestlings were ever seen pecking at the markings. Broods were then video recorded again using infrared cameras for 2 h and 15 min. Nestlings were weighed again in the evening of the day of the experiment, and the partition was removed. The video recordings were used to determine food provisioning by male or female to individual nestlings, with the observer being blind to the identity and the treatment of individual nestlings. Number of prey items received was used to estimate food allocation because it was shown to reflect quite precisely the quantity and quality of the food given to a nestling (McCarty 2002). The begging level of all nestlings was recorded at each feeding event in a subsample of 18 nests. Begging scores were measured using the following scale: 0 = calm; 1 = weak gaping; 2 = persistent gaping; 3 = gaping, neck fully stretched; 4 = gaping, neck fully stretched, wing flapping (Kölliker et al. 1998). Average begging scores were calculated for each nestling over the duration of the whole record and this average per-nestling begging score was used in the statistical analysis of begging intensity. No acoustic measures of begging could be taken due to the technical difficulties involved in obtaining begging call recordings of individual nestlings from within a brood. Mass gain was calculated as the difference in mass between the morning and the evening of the experimental day (time range: 7 h and 50 min–10 h and 25 min). Mass gain was analysed on a longer timescale than begging and food provisioning to obtain a longer-term measure of the differential effect parents may have on their nestlings' growth and due to the difficulty of measuring very small mass differences under field conditions.

Statistical Analysis

The data were analysed with general linear mixed-effects models using R version 2.0.1 (R Development Core Team 2004). The dependent variables in separate models were the number of food items given to a nestling, the nestling mass gain and the average begging score of nestlings. To take into account the nonindependence of nestlings raised in the same nest, the variable nest was included as a random factor in every model (Pinheiro & Bates 2004). The hunger manipulation (i.e. hungry or unmanipulated), the sex of the feeding parent (corresponding to the experimental brood division; see above) and their interaction were included as fixed factors. Furthermore, hatching date, brood size and sex of nestling were included in all models as covariates. Premanipulation body mass was also included in the analysis of begging intensity. Begging intensity was used as a covariate in the analyses of food provisioning and mass gain to test for an effect of hunger and parental sex that would not be mediated by begging posture. The dependent variables were transformed when the assumptions of normality and homoscedasticity were not met. Covariates and the interaction between hunger and parental sex were backward eliminated when clearly nonsignificant ($\alpha = 0.1$). For variables that showed a tendency towards significance ($0.1 > P > 0.05$), we also used a model selection approach, calculating the AIC to decide whether these variables could be safely eliminated (Pinheiro & Bates 2004; Stephens et al. 2007). When this criterion, which is smallest in the best model, was very similar in both the models with and those without a specific variable, both models are discussed and compared since they are statistically equivalent (Pinheiro & Bates 2004). As the question of whether males and females responded similarly to hungry nestlings on their respective side was of central importance and part of the objective of the study, we also present AIC for models with and without the interaction between parental sex and nestling hunger, irrespective of the resulting P value. The AIC was also used to support the conclusion of a lack of a long-term harmful effect of the hunger manipulation on body mass. Indeed, we found no long-term effect of food deprivation on nestling mass because body mass at the end of the experimental day was not different in food-deprived and control nestlings ($F_{1,148} = 0.64$, $P = 0.42$; AIC with/without: 643/640). This manipulation thus had only a short-term effect on nestlings. In addition, we observed no case of parental desertion.

RESULTS

Begging Intensity

Food-deprived nestlings begged at significantly higher intensities than their unmanipulated siblings (Fig. 1; $F_{1,96} = 12.2$, $P < 0.001$). Nestlings on the female side begged more intensely than those on the male side ($F_{1,96} = 5.8$, $P = 0.017$) irrespective of their food deprivation treatment (interaction food deprivation × parental sex: $F_{1,95} = 0.09$, $P = 0.76$). Begging rate did not vary with nestling sex ($F_{1,96} = 0.002$, $P = 0.97$) or brood size ($F_{1,15} = 0.04$, $P = 0.84$) but decreased slightly with nestling body mass ($F_{1,96} = 4.1$, $P = 0.047$).

Food Distribution

As expected food-deprived nestlings were fed at higher rates than their siblings (Fig. 2; $F_{1,148} = 16.8$, $P < 0.001$), on both the male and the female sides of the nest (interaction food deprivation × parental sex: $F_{1,146} = 0.32$, $P = 0.56$; AIC with/without: 483/480). Females and males provided food at similar rates ($F_{1,148} = 3.5$, $P = 0.061$; AIC with/without: 480/479). When begging was included in the statistical model we found a marginally nonsignificant effect of the interaction between the sex of the feeding parent and the begging level on food provisioning ($F_{1,96} = 3.9$, $P = 0.051$; AIC with/without: 277/277). Indeed the relationship between begging and food provisioning was significant and positive in males ($F_{1,40} = 36.2$, $P < 0.001$) but not in females ($F_{1,40} = 0.97$, $P = 0.33$). The effect of the hunger manipulation on food provisioning remained highly significant ($F_{1,96} = 15.1$, $P < 0.001$).

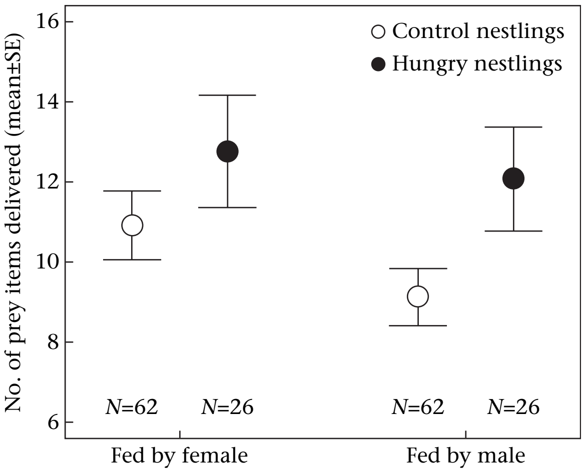

Figure 2. Food provisioning by males and females to food-deprived and control nestlings.

Mass Gain

In control nestlings, increase in body mass was slightly although nonsignificantly higher on the female side of the nest than on the male side (Fig. 3; $F_{1,97} = 2.92$, $P = 0.09$; AIC with/without: 360/359), whereas food-deprived nestlings gained mass similarly on both sides ($F_{1,25} = 0.37$, $P = 0.54$; Table 1; interaction food deprivation × parental sex: $F_{1,147} = 2.97$, $P = 0.087$; AIC with/without: 218/217). As shown by the close AIC values, the two models, with and without the interaction, are statistically equivalent and thus both are given here. When the interaction was removed from the model (Table 1), food-deprived nestlings increased more in body mass than their siblings ($F_{1,148} = 26.8$, $P < 0.001$) and nestlings fed by males and females did not differ in their mass gain ($F_{1,148} = 0.82$, $P = 0.37$). Begging posture was not kept in the model as a covariate because there was no trend for a relationship between begging posture and mass gain ($F_{1,97} = 1.38$, $P = 0.24$).

DISCUSSION

Our study shows that both males and females fed hungry nestlings preferentially when nestling choice between approaching the male or approaching the female parent

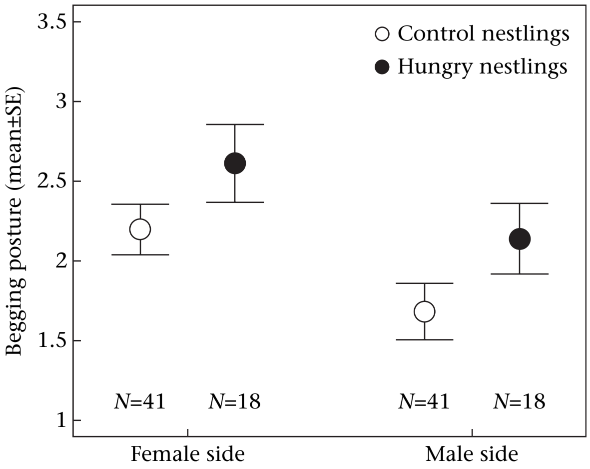

Figure 1. Mean begging posture of food-deprived and control nestlings when fed by male or female parents.

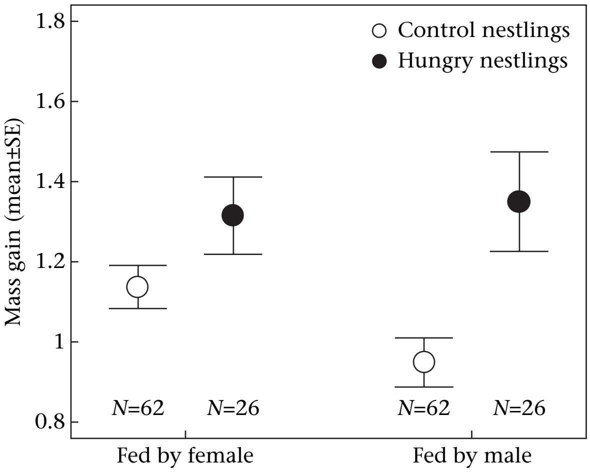

Figure 3. Mass gain of food-deprived and control nestlings when fed by male or female parents.

Table 1. Summary of the statistical analysis showing the variables that influence nestling mass gain for the model including the interaction between hunger manipulation and sex of the feeding parent and the model without the interaction

Variable	Value	*df*	*F*	*P* value
Model with interaction (AIC=218)				
Intercept	−1.002	147	2.192	0.141
Hunger	0.214	147	6.235	0.014
Parental sex	−0.111	147	2.896	0.091
Date	0.042	24	9.542	0.005
Hunger*parental sex	0.207	147	2.973	0.087
Model without interaction (AIC=217)				
Intercept	−1.031	148	2.326	0.129
Hunger	0.317	148	26.838	0.000
Parental sex	−0.050	148	0.819	0.367
Date	0.042	24	9.536	0.005

Variables that are not mentioned in the table were not significant and therefore were removed from the models.

was experimentally restrained. Females and males showed a similar preference to allocate a higher proportion of their feedings to food-deprived nestlings. This result and the previously found higher female provisioning rate to hungry nestlings under conditions where the nestlings were unconstrained in their positioning (Kölliker et al. 1998) suggest that the active positioning choices of nestlings play a critical role in the competitive dynamics among nestling birds. Choice by nestlings implies that they can assess the profitability of different locations in the nest and position themselves accordingly. This is supported by the previous finding that nestlings can learn their parents' feeding positions in the nest (Kölliker & Richner 2004; Budden & Wright 2005). Nestlings thus have at least partial control over food distribution by their option to compete with nestmates for space nearby parental feeding locations (McRae et al. 1993; Kölliker & Richner 2004).

Kölliker et al. (1998) hypothesized that obtaining food from the male parent may be more costly because in their study nestlings fed by the father were begging at higher rates than those fed by the mother, and fathers showed a higher latency before feeding. We found that nestlings on the female side begged with higher intensity than those on the male side, as was also found in barn owls, *Tyto alba* (Roulin & Bersier 2007). Furthermore, the parental responsiveness to begging appeared different for males and females, as suggested by a significant correlation between food provisioning and begging in males but not in females. Unpublished correlational data from the study by Kölliker et al. (1998), where nestlings were free to position themselves, previously suggested that females used food provisioning rules different from those of males. Females appeared to modify their response to begging intensity in relation to nestling position by discounting begging intensities of closer nestlings, while males responded to begging posture and position independently (M. Kölliker, unpublished). Thus, because in the present study the nestlings were experimentally constrained to be near the female or the male, a given level of begging might have elicited less provisioning on the female side than on the male side, and nestlings might have been required to intensify their begging as a result to maintain food intake on the female side. In addition, with regard to body mass, the effect of parental sex on change in body mass appeared not to be simply mediated by begging. Indeed, despite higher begging levels and slightly (not significantly) higher overall provisioning rates by females, food-deprived nestlings gained mass similarly on both sides of the nest. Contrary to our expectation, it thus seems advantageous for hungry nestlings to be fed by their father given the constraint to be at close proximity to the feeding parent, at least in terms of short-term body mass gain. A potential explanation for the discrepancy between begging, food provisioning and nestling mass gain is begging costs. If begging is energetically costly (Kilner 2001), nestlings fed by the father could gain body mass similarly, despite the lower food provisioning, due to decreased energy expenditure in begging behaviour at the male's side. Alternatively, males might provision control and food-deprived nestlings differentially with regard to food quality, leading to increased mass gain of hungry nestlings. However, we know of no study that would show such subtle differences in the feeding strategies of males and females. Finally, it was previously found that the vocal part of begging affected mainly parental feeding rates, whereas visual displays had an effect on food distribution by parents among nestmates (Glassey & Forbes 2002). Similarly in our study the visual begging components partly explained the variance in food distribution, leaving room for other begging components and subtle parental decisions to influence food distribution. There might, for example, be a trade-off in the investment in visual and vocal components of begging as in parasitic cuckoo nestlings (Kilner et al. 1999). In that case hungry nestlings fed by the father might have increased their vocalization at the expense of posturing. In tree swallows, *Tachycineta bicolor*, it was indeed found that nestlings adjusted calling rate and posturing independently as distance from feeding locations was experimentally increased (Leonard et al. 2003).

The discrepancy between our results and those of Kölliker et al. (1998) might also partly be explained by a differential sensitivity of male and female provisioning decisions to the external ecological conditions (Johnstone & Hinde 2006). Males generally are hypothesized to invest less time and energy in parental care and therefore to feed only the nestlings that provide the highest fitness return at the lowest possible cost (Slagsvold et al. 1995). However, feeding strategies of caring adults towards small and large young can change according to environmental conditions, such as food availability (Boland et al. 1997) or time in the season (Bize et al. 2006). In addition, males and females may respond differently to changes in environmental conditions as shown in crimson rosellas, *Platycercus elegans*, and canaries, *Serinus canaria*, where females, but not males, altered their feeding behaviour in favour of bigger nestlings under experimental manipulation of brood hunger state (Krebs & Magrath 2000; Kilner 2002).

In several bird species, nestlings increase their begging rate when food deprived (Smith & Montgomerie 1991; Kilner & Johnstone 1997; Leonard & Horn 2001a; Quillfeldt

2002; Sacchi et al. 2002), and parents generally increase food provisioning in response to experimental food deprivation of nestlings (Kilner & Johnstone 1997; Leonard & Horn 1998) or to begging playbacks (Bengtsson & Rydén 1983; Burford et al. 1998; Leonard & Horn 1998, 2001b). Likewise, in our study, parents were sensitive to nestling hunger when providing food. In addition to nestling hunger, competitive abilities may influence begging levels (Rodriguez-Girones et al. 1996) because of a difference in the cost of begging for big and small nestlings (Parker et al. 1989; Godfray 1991). Thus, begging behaviours may often reflect offspring need (Price et al. 1996; Saino et al. 2000) or physical condition (Lotem 1998), but most probably in many cases a combination of both (Kilner & Johnstone 1997). It thus may be adaptive for females to modulate their response to begging with nestling phenotype. In addition and as shown in this study, begging does not reflect just nutritional condition or competitive ability but may also be influenced by some unknown behavioural or other properties of the parent in their interaction with the nestlings.

In summary, we found that nestling great tits play a significant role in the distribution of food through two different mechanisms. First, they compete for profitable positions in the nest cup by jockeying with their nestmates. Second, they can adjust their begging intensity to their present position in the nest. Thus, nestlings are interacting with their parents in a very subtle manner.

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