

University of Groningen

Reproductive decisions in great tits

Verhulst, Simon

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

1995

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Verhulst, S. (1995). Reproductive decisions in great tits: An optimality approach s.n.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

The problem studied in this thesis is the origin and maintenance of phenotypic variation in behaviour, in particular reproductive behaviour of Great Tits *Parus major*. The reproductive decisions studied are laying date, clutch size and whether or not to start a second clutch after rearing the first brood. A schematic overview of the main relationships that could be established experimentally is presented in Figure 1.

With respect to laying date it was investigated whether the seasonal decline in reproductive success that is generally observed can be attributed to variation in quality between early and late breeders, or whether the decline was causally related to seasonal variation in the environment (4*). It was concluded that the seasonal decline in reproductive success was largely due to time rather than quality.

The experiments with laying date were carried out in Oosterhout, a woodland near Nijmegen in the Netherlands. All other studies in this thesis were carried out on Vlieland, an island in the Dutch Waddensea. This population is relatively isolated, which is reflected in the low proportion of immigrants as compared with other populations (2). Genetically, the population is slightly more isolated than suggested by the immigration rates, because the lifetime production of (local) recruits was reduced in female immigrants, as compared with females hatched on Vlieland.

The relationship between fitness and natural variation in clutch size was evaluated for the Vlieland population (3), and the results were somewhat unexpected. Females laying large clutches enjoyed a lower lifetime production of local recruits than females laying an intermediate number of eggs, while in other populations (e.g. De Hoge Veluwe, Wytham) large clutches are associated with

high reproductive success. This analysis was followed up with an experimental study in which clutch size was experimentally reduced, and reproductive success was compared between experimental birds and unmanipulated control birds (5). To my surprise the experimental reduction in clutch size resulted in an increase in reproductive success. It is therefore concluded that clutch size of Great Tits breeding on Vlieland is maladaptive. Gene flow from other populations could possibly explain this result, and it was found that immigrant females laid larger clutches than females hatched on Vlieland, which lends some support to this suggestion (5).

The main reason for the increase in reproductive success following an experimental reduction in clutch size was enhanced output from second clutches. Pairs with an experimentally reduced clutch were more likely to start a second clutch and these second clutches were also more successful. It is not yet clear what causes the effect of the number of young in the first brood on the occurrence and success of second clutches. Energy expenditure of males and females rearing control and experimental broods was measured using doubly labeled water (6), but no correlation was found between energy expenditure and the occurrence of second clutches. This suggests that the effect of the clutch size manipulation on second clutches is not mediated by an effect of brood size on work rate of the parents.

It has previously been hypothesized that pairs with an experimentally reduced clutch could spend less time on post-fledging care, and thereby have more time left in the season to rear a second clutch. The duration of post-fledging care was studied (7), but there was no detectable effect of the clutch size manipulation on the duration of post-fledging care. It is suggested that second clutches could have an effect on the fitness of the first clutch, since second clutches could be shown to

* Numbers in brackets refer to Chapters.

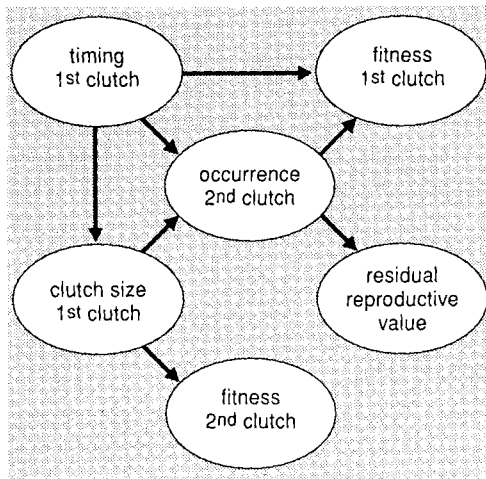


Figure 1. Schematic overview of the main relationships between reproductive decisions and fitness components that could be established experimentally in this study. All relationships are negative. With 'Fitness 1st Clutch' (or 2nd clutch) the contribution of the first (or second) clutch to the reproductive value of the parent is implied.

interfere with post-fledging care. Such an effect could be stronger in large clutches, which could potentially explain why pairs with small clutches are more likely to start a second clutch. It could be shown by removing second clutches that second clutches have an adverse effect on the fitness of first clutches (8), which supports this hypothesis. Further experimentation is required to establish whether this effect is stronger for large first broods than for small first broods.

The clutch size manipulation did not affect parental survival until the next breeding season. Although experimental pairs reared fewer young in their first brood, they invested more in second clutches which could explain the absence of an experimental effect on parental survival. This possibility was investigated experimentally by removing second clutches (9), which enhanced future reproductive output (survival, fledgling production). Thus the costs of rearing a second clutch may explain why pairs of which the first clutch was experimentally reduced did not enjoy higher survival rates.