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Institute for Ecological Research, Heteren, Holland

The influence of winter severity on Coot (*Fulica atra*) dispersal*

By Albert C. Perdeck

1. Introduction

This paper deals with dispersal of Coot breeding in The Netherlands. Recoveries of, and observations on marked individuals show that many birds stay at the breeding grounds during winter, but at the same time others were recovered far away, up to 1500 km from the breeding place. During cold winters there is increased mortality among the sedentary individuals (VISSER 1978), and the mean survival rate of a well-studied population varies negatively with the coldness of the winter (CAVÉ & VISSER 1985).

This gives rise to questions like: Why stay some birds near the breeding grounds even when conditions are bad? Is the degree of dispersal related to such conditions? Or more general: which factors determine the residency/migratory habit of an individual bird? Is this habit fixed genetically or is it acquired and fixed during life? Or does the individual just react to the momentary circumstances with the most appropriate behaviour?

The aim of this paper is to give a contribution to this problem by an analysis of ringing recoveries in relation to winter severity.

2. Material and methods

The 78 recoveries used for this analysis have been selected from all available recoveries of Coot ringed in the Netherlands, and refer to 59 recoveries of birds in their first winter (young birds), and to 19 recoveries of birds in their second or later winters (old birds). The material is restricted to those birds that were either ringed as chicks, or as full-grown birds from April through September, and shot (75) or caught intentionally (3) in December, January or February.

Recoveries at or near the ringing place have been omitted. They probably have an abnormal and varying reporting rate. Local hunters may be informed about the ringing programme and report directly to the ringers. We know that this is the case for the Coot project of our institute from which the majority of the recoveries originate. More serious, however, is that in this project the recoveries of birds shot near the ringing place come mainly from one hunter who shot irregularly, i. e. a great deal in some winters, and not at all in others (J. VISSER, pers. comm.). It is likely that the shooting activity was reduced during severe winters when the birds were fed by the general public.

Recoveries of shot birds are more suitable for this analysis than those of the other main category "found dead", because recoveries in the latter category are all close to the ringing place. This is probably caused (1) by a high reporting rate in our densily populated country, and (2) by a high mortality during cold spells in the area where the temperature was measured, i. e. near the breeding place. By using the "shot" recoveries, on the other hand, the "migration" will be exaggerated (CAVÉ 1968), since shooting rate is comperatively high in France, from where most of the long-distance recoveries originate. Lumping together both categories is therefore impermissible when studying distance-related problems (PERDECK 1977, PERDECK & CLASON 1982).

As a measure of dispersion the loxodromic distance between the geographical coordinates of the ringing and finding place is taken, called recovery distance.

* Based on a lecture given on the occasion of the 75th anniversary of the Vogelwarte Helgoland, April 5th, 1985, Helgoland.

Table 1: Kendall rank correlations between recovery distance when shot and coldness during periods of increasing length previous to date of shooting.

Tab. 1: Kendall-Rang-Korrelation zwischen der Wiederfundentfernung beim Abschuß und der Kälte in Zeitabschnitten zunehmender Länge vor dem Abschuß.

COLDNESS OF PERIOD	1st WINTER BIRDS (n = 59)		OLDER BIRDS (n = 19)	
	corr. coeff.	P (two-tailed)	corr. coeff	P (two tailed)
D0	- 0.19	0.04	- 0.05	0.75
D0 + D-1	- 0.21	0.02	0.06	0.72
D0 + D-1 + D-2	- 0.17	0.06	0.07	0.70
D0 + D-1 + D-2 + D-3	- 0.12	0.17	0.10	0.55

D0 is coldness (Hellmann number) of decade when shot.
D-1 is coldness (Hellmann number) of decade previous to D0 decade, etc.

The severity of a certain winter is defined as the absolute sum of all negative daily mean temperatures (C), measured at De Bilt, in the middle of the Netherlands. This figure is known as the Hellmann number. For relating recovery distance to the severity of the winter in which the bird was shot, Hellmann numbers of decades within the month are used (Climatology 1985).

3. Severity of winter and recovery distance during the same winter

Recovery distance when shot has been related to the coldness of various periods before the date of shooting. The Hellmann number for the decade in which the bird was shot is called D0, and those for the three previous decades D-1, D-2, D-3, respectively. Kendall rank correlations were calculated between recovery distance and D0, recovery distance and (D0 + D-1), recovery distance and (D0 + D-1 + D-2), and between recovery distance and (D0 + D-1 + D-2 + D-3). The result is given in Table 1, for young and old birds separately. Coot react in their first winter especially to (D0 + D-1), but in a negative way. (Fig. 1). This means that during cold spells the recovery distance is smaller. Old birds do not react at all to temperatures, their recovery distance remains more or less constant (Fig. 1).

The negative relationship in the young birds is unexpected. Tentatively it might be explained as follows. During cold weather the food availability is reduced. Lawns are covered with snow and waters are frozen. The birds are grouping together on the few feeding places still accessible and defence of territories is given up. This gives the young birds an opportunity to come closer to the breeding area. After the cold spell the food becomes available everywhere again and the young birds may be driven out again to regions farther away. In the discussion more support for these speculations will be given.

4. Severity of winter and recovery distance during the next winter

It is of interest to explore the influence of the previous winter on the recovery distance in the present one. Depending on the severity of the previous winter the sedentary birds will have survived in smaller or greater numbers. In what way does this affect the distribution in the present winter?

In Fig. 2 the recovery distance of recovery is plotted against the severity of the previous winter for both age categories. In the old birds there is a clear positive correlation ($P = 0.03$).

The adults stay, on average, further away from the ringing area if the previous winter was severe. At first sight there does not seem to be a distinct correlation in case of the young birds. However, there is an outlier from the very severe winter 1962/63. Moreover, the number of recoveries per winter varies greatly, from 1 to 18. Therefore a Kendall rank correlation was applied, resulting in a negative correlation (P = 0.12, two-tailed). When the outlier is left out P reduces to 0.06.

An explanation for the positive relationship in the old birds between recovery distance and coldness of the previous winter is that many birds staying close to the breeding area died in that winter. Vacancies thus created have, in the subsequent winter, not been occupied by surviving old birds. The latter seem to be faithful to their wintering place of the previous year. It is possible, then, that the first-year birds are candidates for the vacancies. In that case one would expect a negative relationship between recovery distance and severity of the previous winter, and this is in fact what the data suggest.

In our argument this relationship is an indirect one. The young birds do in fact react to the density distribution of the old birds. This distribution is a result of the survival in the previous winter. The direct relationship can be tested by relating the recovery distance of the young birds in a certain winter to the recovery distance of the adults in the same winter. In Fig. 3 the mean recovery distance of the first-winter birds is plotted against the mean recovery distance of the older birds, separately for each winter, from which at least one recovery from each age category was available. There is a distinct negative relationship (P = 0.02). This supports the idea that the young birds indeed take over the places left vacant by the old birds whenever this is possible.

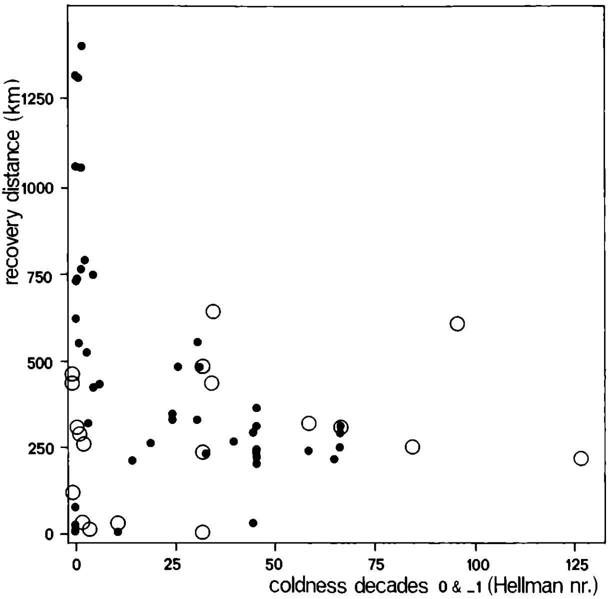

Fig. 1: Recovery distance during winter in relation to temperature in the same winter. As temperature is taken the Hellmann number of both the decade that the bird was shot as the one before that. Hellmann number is the absolute sum of all negative daily mean temperatures (C), measured at De Bilt. Small dots: first-winter birds. Circles: older birds.

Abb. 1: Wiederfundentfernung im Winter in Bezug zur Temperatur im selben Winter. Als Temperatur wurde die Hellmann-Zahl der Dekade vor und in der der Vogel geschossen wurde, gewählt. Die Hellmann-Zahl ist die Summe aller negativen Tagesdurchschnittstemperaturen in °C, die in de Bilt gemessen wurden. Kleine Punkte: Vögel in ihrem ersten Winter. Kreise: ältere Vögel.

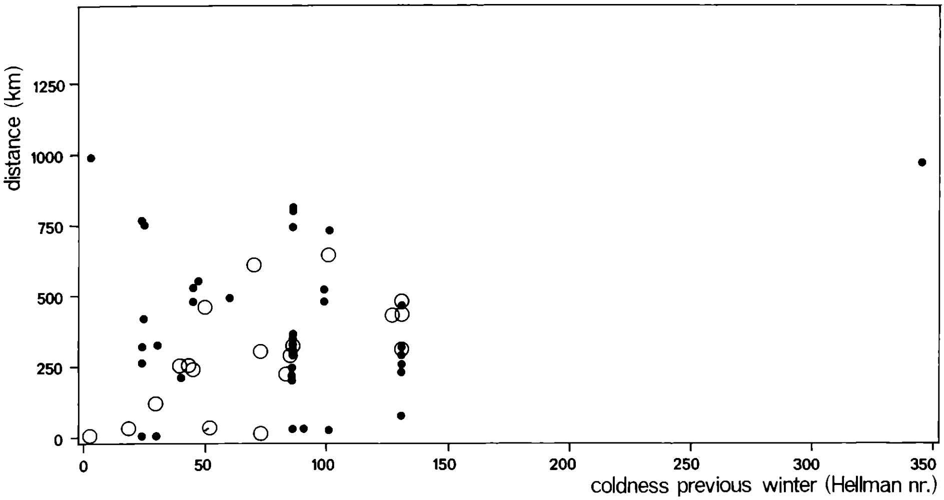

Fig. 2: Recovery distance during winter in relation to temperature of the foregoing winter. As temperature is taken the Hellmann number of November through March. Hellmann number is the absolute sum of all negative daily mean temperatures (C), measured at De Bilt. Small dots: first-winter birds. Circles: older birds.

Abb. 2: Wiederfundentfernung im Winter in Bezug zur Temperatur im vorigen Winter. Als Temperatur wurde die Hellmann-Zahl der Dekaden von November bis März gewählt. Die Hellmann-Zahl ist die Summe aller negativen Tagesdurchschnittstemperaturen in °C, die in de Bilt gemessen wurden. Kleine Punkte: Vögel in ihrem ersten Winter. Kreise: ältere Vögel.

5. Discussion

The results of the present study indicate that Coots try to overwinter as close to their breeding grounds as possible. In their first winter the young birds have to compete with older ones. Localities on or near the breeding grounds are likely to be occupied by these old birds, but it is suggested that during cold spells their competitive behaviour is weakened, thus creating an opportunity for the young to come nearer. Support for this idea comes from SABINE (1959) and PULLIAM et al. (1974) who found a negative relationship between tolerance of proximity and temperature in foraging Juncos during winter. Further, MARLER (1956) and WILEY & HARTNETT (1979) experimentally showed that acute deprivation from food increased individuals' tendency to approach other individuals at food in Chaffinches and Juncos.

Although after a cold period the adult Coots seem to regain their rights, it is likely that some young can benefit from the situation, and take hold of a place nearer to the breeding grounds than would have been possible if they had stayed away. Admittedly, this advantage has to be balanced against the greater risks involved in approaching the breeding grounds under adverse conditions.

After a hard winter many of the birds staying near the breeding area have died, the risk that has to be taken in an unpredictable climate. As a result, vacant overwintering localities, especially near the breeding area, will become available in the next winter, while after a mild winter vacant places are more distant. Such vacancies are likely to be occupied again the next winter. The old birds are probably tied to the place where they stayed the previous winter. Fidelilty to wintering sites is common in birds. The resulting familiarity with the place enhances feeding and shelter efficiency, but also dominance over individuals not familar with the surroundings (SABINE 1949, HINDE 1953, DRENT 1983).

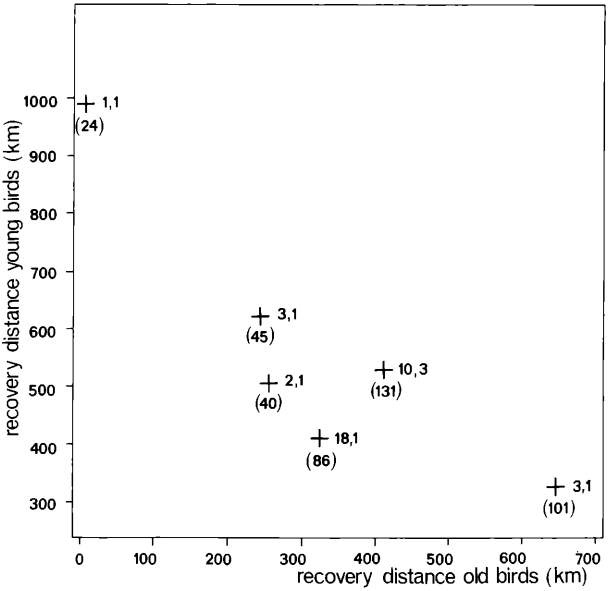

Fig. 3: Mean recovery distance of first-winter Coots in a certain winter in relation to mean recovery distance of older Coots in that same winter. The two figures next to the signs indicate the number of recoveries of first-winter and older birds resp., on which these means are based. The figure in brackets is the Hellmann number of severity of the winter concerned.

Abb. 3: Durchschnittliche Wiederfundentfernung aller Bläßhühner in ihrem ersten Winter in Bezug zur durchschnittlichen Wiederfundentfernung älterer Bläßhühner im selben Winter. Die beiden Zahlenangaben neben den Markierungen bezeichnen die Anzahl der Wiederfunde erstjähriger bzw. älterer Vögel, auf denen die Durchschnittswerte basieren. Die Zahl in Klammern ist die Hellmann-Zahl, die die Strenge des betreffenden Winters charakterisiert.

In the Coot, the existence of fidelity to wintering grounds has been demonstrated experimentally by RÜPPELL & SCHIFFERLI (1939). They displaced Coots, wintering in Switzerland, to Berlin, 655–700 km NE. In the same winter, from a group of 16 birds, conspicuously marked with a white painted neckband, 5 returned to exact the same wintering place. Some birds stayed near Berlin during the same winter, and one was still observed there in the third winter after the experiment. The age of the birds was unknown, but the authors suggest that the first-winter birds had not yet developed the site fidelity to a winter quarter. This is in accordance with other experiments, e. g. with Starlings, Chaffinches and Teal (PERDECK 1958, 1967; WOLFF 1970). After sideways displacement in autumn off the migration route, the adults migrated directly toward their original winter quarters, but the first-year birds continued in the normal migration direction. Displacements during winter with Northern Waterthrushes *Seiurus noveboracensis* (SCHWARTZ 1963) and Sparrows *Zonotrichia* species (RALPH & MEWALDT 1976) also demonstrated a stronger fixation to the winter home in adults, when compared to young birds. RALPH & MEWALDT (1975) produced evidence that in the young birds this fixation increased with time in the first winter. This leads us to suggest that the vacancies in the wintering area will be occupied mainly by the first-winter Coots. This is, however, only poorly demonstrated by the data.

A difficulty is the absence of long-distance recoveries of old birds (Fig. 1). If it is true that the attachment to a wintering place is completed after the first winter one would expect long-distance recoveries also in later years. Here a general problem is met. From recoveries of ringed birds it has often been concluded that juveniles migrate farther away than adults (e. g.

LACK 1944). However, there are two possible explanations for such a pattern in recoveries of ringed birds. One is that the birds indeed migrate to more distant places during the first winter, but stay nearer in subsequent ones. Another explanation is that the recovery distance is related to the position in the rank order of dominance, and that the birds that overwinter at great recovery distance are the most subordinate individuals with the lowest survival rate. In this view the high mortality of first-year Coots (CAVÉ & VISSER 1985) is due especially to the long-distance migrants, resulting in reducing the mean recovery distance in later years. This mechanism might, by the way, explain the larger recovery distances in the juveniles of other species too.

Moreover, it is possible that attachment to a winter locality is not always completed after the first year. Displacement experiments (PERDECK 1958) showed that some of the autumn-displaced first-year Starlings returned to the new wintering area in later years, while others returned to the original winter quarters. If there is a general tendency to stay close to the breeding area, attachment in second winters will be at shorter recovery distances.

Another question to be elucidated is whether recoveries up to 1500 km can be explained by spatial competition only. This seems unlikely, but it is possible that once low-rank individuals become adrift, some general migration threshold is surpassed. They might also join migrant populations from Northeast Europe. TOWNSHEND (1985) could relate extended migration of individual juvenile Grey Plovers to competition at a site close to the breeding area. He also showed that patterns of seasonal movements, established during competition, were fixed for life in the individual. PIENKOWSKI & EVANS (1986) give evidence that in shorebirds there is competition amongst juveniles, and between juveniles and adults, for winter sites which minimize the recovery distance juveniles have to migrate from their birthplaces, thus reducing the cost of migration.

In summary it seems possible to explain the dispersion of Coots breeding in the Netherlands by competition for winter quarters close to or even at the breeding grounds during the first winter, followed by site fidelity in later winters. This implicates that the residency/migratory habit or the distance of migration of an individual may not be fixed genetically, but determined phenotypically in its first year of life. Thus partial migration in the Coot cannot be explained by BERTHOLD's (1985) genetic hypothesis of partial migration, although there might be an inborn faculty to migrate in a certain direction, aroused under certain conditions. More suitable seems GAUTHREAUX' (1978, 1982) dominance-dispersal model. It relates winter dispersal directly to competition for resources. The birds are not supposed to be tied very much to their winter sites. They may therefore react to decreasing resources (e.g. due to falling temperatures) by moving to more suitable places. During this process the juveniles migrate farthest away from the breeding quarters, due to their subordinate position.

The latter seems to be the case in the Coot also. Distant winter sites occur in the first winter of an individual only. Their absence in later winters can be explained by high mortality of the most subordinate and most dispersed birds. But in other aspects the studied population seems to be different from Gauthreaux' model. Winter-site fidelity seems of such importance, that an individual is condemned to a site for its life. If this winter site is not close to the breeding site of the individual no correction seems to be possible and either the bird is a loser or it has to adapt a migratory strategy. The indication that juveniles try to move closer to the breeding grounds during winter even under adverse wheather suggest that a shortening of the migration distance is essential. This might have to do not only with the benefits of early arrival at the breeding grounds, but also with the reduction of migration costs for a lifetime. In the Coot these costs are probably high, due to high flying costs (relative small wing area, high wing beat rate). Therefore is might pay for the young birds to approach the breeding quarters, and for the old birds to stay on or near these quarters, even under hazardous conditions.

6. Acknowledgements

The idea of relating the recovery distance in a certain winter to the severity of the foregoing winter was suggested to me by Dr. A. J. Cavé. The interpretation of the data was clarified during discussions with him and with Prof. Dr. R. H. Drent and Dr. J. M. Tinbergen. Computer programs were written by Mr. C. Clason.

Summary

The influence of temperature on wintering position was studied in Coots breeding in the Netherlands, using recoveries of ringed birds. Position was defined as recovery distance between place of ringing and place of recovery (birds shot in December, January and February, recoveries at ringing locality excluded). A distinction was made between birds in their first winter (young) and in later winters (old). Temperature was defined as the absolute sum of all negative daily mean temperatures of decades in November through March.

Recovery distance depended on temperature of the two decades preceding date of recovery in young, but not in old birds (Table 1, Fig. 1). This dependency was not positive, as would be expected if the young birds tried to escape from the cold, but negative, indicating that under adverse conditions the young come nearer to the breeding grounds. Tentatively, this is explained by a relaxation of territorial defense by the old birds wintering on or near their breeding place. This creates an opportunity for the young to obtain a place for overwintering closer to their future breeding place, a benefit to be weighted against the risk of dying due to factors related to the cold. When the cold spell is over this opportunity is lost, and the young that have not been able to secure a place nearby are driven away again.

The idea that a young bird tries to obtain a favourable starting point during its first winter is supported by the dependency of the recovery distance in a certain winter on the coldness of the previous winter (Fig. 2). This relationship is clearly positive in the old birds, and can be understood by mortality of birds overwintering near the breeding area (where the temperature is measured), in combination with lifetime site fidelity to the winter locality. After a severe winter the mortality is high in the more sedentary birds and, due to their winter-site fidelity, the surviving more migratory individuals do not replace the ones that have died. As a result the mean recovery distance after a severe winter is larger than after a mild winter.

If the old birds that have died are not replaced by surviving old ones, one would expect a replacement by young birds, that have not yet been tied to a certain winter locality. This might indeed to be the case, since after a severe previous winter the young birds tend to stay closer to the place of ringing than after a mild winter, although the evidence is weak. This suggests that when the old birds are nearby during a certain winter, the young are farther away and vice versa. The rather scanty data available to test this negative relationship are confirmatory (Fig. 3).

In conclusion, the data presented are in accordance with the idea that Coots try in their first winter to obtain a wintering place as close as possible to their future breeding grounds, and that they are faithful to it in later winters. The acquirement of this place seems to occur even under adverse conditions like cold spells in winter, and this suggests that a reduction of recovery distance between wintering and breeding place is of paramount importance. This might be due not only to the general advantage of having early access to a breeding territory, but also to the high energy costs of flying, typical for the species.

The partial migratory behaviour of the population studied is not easy to reconcile with a model explaining partial migration by a genetically determined polymorphy.

7. Zusammenfassung

Der Einfluß der Winterhärte auf das Wintervorkommen des Bläßhuhns

Der Temperatureinfluß auf die Winteraufenthaltsorte der in den Niederlanden brütenden Bläßhühner wurde anhand von Wiederfunden beringter Vögel untersucht. Aufenthaltsort wird hier definiert als die Entfernung zwischen Beringungs- und Wiederfundort im Dezember, Januar und Februar von geschossenen Vögeln; ausgenommen hiervon sind die am Beringungsort wiedergefundenen. Es wurde zwischen Vögeln in ihrem ersten Winter und älteren Vögeln unterschieden. Als Temperatur wurde die Summe aller negativen Tagesdurchschnittstemperaturen der Dekaden von November bis März bestimmt.

Die Wiederfundentfernung der Jungvögel, nicht aber der Adulten, wurde von der Temperatur in den beiden Dekaden vor dem Wiederfund beeinflußt (Tab. 1, Abb. 1). Es gab jedoch keine positive Korrelation, die man erwartet hätte, wenn Jungvögel vor der Kälte fliehen würden, sondern eine negative, die darauf hindeutet, daß die Jungvögel bei ungünstiger Witterung näher zum Brutort ziehen. Als Erklärung wird vorgeschlagen, daß die Territorienverteidigung der Adulten nachläßt, die am Brutort oder in dessen Nähe überwintern. Dadurch erhalten Jungvögel die Gelegenheit, näher zum zukünftigen Brutort zu überwintern. Diesem Vorteil wirkt das Risiko entgegen, aufgrund von Kälteeinflüssen zu sterben. Wenn der Kälteeinbruch vorbei ist, werden die Jungen, die nicht in der Lage waren, sich in der Nähe einen Platz zu sichern, wieder vertrieben.

Es besteht eine Korrelation zwischen der Wiederfundentfernung in einem bestimmten Winter und der Kälte im vorhergehenden Winter (Abb. 2). Dies stützt die Vorstellung, daß ein Jungvogel versucht, während seines ersten Winters eine günstige Ausgangsposition zu erlangen. Diese Korrelation ist bei Adulten eindeutig positiv und erklärbar durch die Mortalität der Vögel, die in der Nähe des Brutortes (wo die Temperatur gemessen wird) überwintern, angenommen, daß die Vögel dem Aufenthaltsort im Winter ein Leben lang treu bleiben.

In harten Wintern ist die Mortalität bei den standorttreuen Vögeln hoch, und die toten Vögel werden – wegen der vorhandenen Winterquartiertreue – nicht von den überlebenden, weiter wegziehenden Individuen ersetzt. Daraus resultiert eine im Vergleich zu milden Wintern größere durchschnittliche Wiederfundentfernung nach harten Wintern.

Wenn die gestorbenen nicht von überlebenden Altvögeln ersetzt werden, sollte man erwarten, daß dies durch Jungvögel geschieht, die noch nicht an ein bestimmtes Winterquartier gebunden sind. Dies könnte auch tatsächlich der Fall sein, da nach einem harten Winter im Jahr zuvor die Jungen näher am Überwinterungsort bleiben als nach einem milden, aber die Beweise reichen nicht aus. Als Folgerung kann angenommen werden, daß sich Jungvögel weiter entfernt aufhalten, wenn Altvögel im betreffenden Winter in der Nähe bleiben, und umgekehrt. Die wenigen vorliegenden Daten sprechen für diese negative Korrelation (Abb. 3).

Zusammenfassend läßt sich sagen, daß die vorliegenden Ergebnisse mit der Vorstellung in Einklang stehen, daß Bläßhühner im ersten Winter versuchen, ein Winterquartier einzunehmen, das so nahe wie möglich am künftigen Brutort liegt und daß sie diesem Winterquartier in späteren Jahren treu bleiben. Auch unter schlechten Bedingungen (Kälteeinbruch) suchen sie ein solches Winterquartier auf. Dies legt nahe, daß eine Verringerung der Ansiedlungsentfernung zwischen Winterquartier und Brutort von größter Wichtigkeit ist. Das könnte nicht nur aufgrund des Vorteils geschehen, einen frühen Zugang zum Brutterritorium zu haben, sondern auch wegen der hohen Energiekosten, die das Fliegen bei dieser Art verursacht.

Das Teilzugverhalten der untersuchten Population ist nicht leicht mit dem Modell zu vereinbaren, das Teilziehen mit einem genetisch determinierten Polymorphismus erklärt.

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Address of the author: Dr. A. C. Perdeck, Institute for Ecological Research, Boterhoeksestraat 22, NL-6666 GA Heteren, The Netherlands.