Spatial demography of black-tailed godwits
Kentie, Roos

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Source-sink dynamics and predicted growth rate of a shorebird metapopulation in an impoverished agricultural landscape

Rosemarie Kentie, Jos C.E.W. Hooijmeijer, Christiaan Both, Theunis Piersma
Ongoing agricultural intensification forms a threat to many species which depend on traditional man-made landscapes. Conservation schemes were set up to protect or develop small areas of biodiverse farmland, which has led to large-scale mosaics with small areas of good-quality habitat embedded in less suitable areas. As a result, populations are patchily distributed and this may affect their dynamics with some areas acting as sinks (mortality > reproduction) and others as sources (reproduction > mortality). However, depending on the strength of the source and the reciprocal dispersal rates, dispersal from sources to sinks may negatively affect population size in sources. Here we present estimates of local demographic rates for black-tailed godwits (*Limosa l. limosa*) breeding in a 8480 ha study area in the Netherlands based on data collected in 2007-2013. We show that modern monocultures covering 80% of the area acted as sinks in most years, while the 20% wet herb-rich meadows (the biodiverse farmland) in most years sustained a source. A population viability analysis identified first-year survival, followed by adult survival, as the key demographic parameters determining population changes. The dispersal rate from meadows to monocultures, even though it was low and lower than the reverse dispersal, prevented the population on meadows to grow. The predicted population size based on demographic rates correlated with independent field counts. Our findings carry two important general conclusions: (1) using population trends to assess habitat quality without knowledge of dispersal processes may be misleading, especially in human-induced habitats where habitat selection cues may not yet be fully appropriate, and (2) the spatial arrangement of protected meadow-areas should be such that ‘leakage’ from sources to sinks is prevented.
INTRODUCTION

In Europe agricultural lands are recognized to harbour considerable biodiversity (Tscharntke et al. 2005), but ongoing intensification of agricultural practices forms a serious threat (Donald, Green & Heath 2001; Kleijn & Sutherland 2003; Vickery et al. 2004; Stoate et al. 2009; Pe’er et al. 2014). Agricultural intensification leads to habitat degradation with negative effects on many taxa, including insects (Benton et al. 2002), small mammals (Wickramasinghe et al. 2003), plant species (Tilman et al. 2001), and birds (Vickery et al. 2001; Newton 2004). To contain such losses of biodiversity, agricultural areas have been put in the hands of conservation management organisations, while farmers have been subsidized to maintain biodiversity on their properties (agri-environmental measures) (Kleijn & Sutherland 2003; Latacz-Lohmann & Hodge 2003; Whittingham 2007; Conover, Dinsmore & Burger 2011). This has generated a situation in which a small fraction of the agricultural land is now managed in more or less traditional, extensive ways. However, due to the often small size of such specially managed areas, the agricultural landscape has become a mosaic of ‘islands’ with traditional agricultural management in a ‘sea’ of impoverished and intensively-cultivated land (Bennett, Radford & Haslem 2006; Whittingham 2007). This form of fragmentation leads to a patchy distribution of species with downstream effects on populations dynamics (Fahrig & Merriam 1994; Newton 1998).

Patchily distributed populations which are connected through dispersal form a metapopulation (Levins 1969; Hanski 1994). To understand the underlying dynamics of a metapopulation it is necessary to know which subpopulations are sources (where reproduction exceeds mortality), which are sinks (where mortality exceeds reproduction), and how well these subpopulations are connected with each other by dispersal (Pulliam 1988; Hanski & Ovaskainen 2000). Especially for populations of conservation concern it is important to identify source and sink populations for management purposes and recognise its habitat characteristics (Dias 1996; Runge, Runge & Nichols 2006).

It is a challenging task to identify if a population is a source or a sink. Individuals need to be marked and followed throughout their lives. Datasets also need to be long-term, as temporal fluctuations in demographic rates may lead to false assignments with respect to which habitats are sources or sinks (Thomas & Kunin 1999; Nystrand et al. 2010). The observations should have enough detail to allow the estimation of key vital rates such as adult survival, reproduction and juvenile survival (Runge, Runge & Nichols 2006). Because of the large effort needed to collect long-term datasets across large enough areas and multiple subpopulations, relatively few empirical studies on source-sink systems have been published so far (see Contasti et al. 2013; Hernandez-Matias et al. 2013 / Table 1 in Chapter 1), let alone a validation of the modelled population dynamics with actual populations sizes (but see Contasti et al. 2013). Reviews and basic theoretical models of source-sink systems, perhaps not surprisingly, are widely available (for example Pulliam 1988; Howe, Davis & Mosca 1991; Dias 1996; Roy, Holt & Barfield 2005; Runge, Runge & Nichols 2006; Loreau et al. 2013).
For effective conservation it is critical to know how sink populations affect the dynamics of the metapopulation as a whole, when connected with sources through dispersal (Howe, Davis & Mosca 1991; Donovan & Thompson III 2001). Theoretical models suggest that sink populations can be beneficial under certain circumstances. For instance, the overall metapopulation size may be larger and may even prevent extinction if the number of sink populations is small enough to not bring the total population down (Howe, Davis & Mosca 1991), or when the mortality in the sinks does not exceed the surplus production in the sources (Beintema 1986). However, if individuals select sinks over sources (Kristan 2003; Battin 2004), or if the proportion of sink habitat is high and individuals select habitats in proportion to their availability (Donovan & Thompson III 2001), the metapopulation may go extinct because too many individuals from sources 'leak' to sink populations.

A bird species of agricultural landscapes of particular conservation concern is the black-tailed godwit of continental Europe (*Limosa l. limosa*). Over the last 50 years their numbers have declined with three-quarters (Gill *et al.* 2008; Boele *et al.* 2013), and this is especially so in the Netherlands which holds over 80% of the continental European population (Piersma 1986; Thorup 2006). The main reason for the loss has been the transformation of their preferred breeding habitat (wet herb-rich meadows) into modern grassland monocultures, areas where first mowing of the year occurs during the incubation period (Schekkerman, Teunissen & Oosterveld 2008; Kleijn *et al.* 2010; Chapter 2; Chapter 4; Chapter 3). Despite the high level of public vigilance from the very start of the population decline, and the resulting conservation measures such as agri-environmental schemes (Kleijn *et al.* 2001; Verhulst, Kleijn & Berendse 2007), numbers of breeding pairs kept on declining. A detailed demographic analysis of source-sink dynamics has not been made.

In this study we present a data set (2007–2013) collected to investigate whether the population breeding on herb-rich meadows within the modern grassland monocultures serve as sources for the population breeding on modern agricultural fields. We analysed key components of population demography by estimating nesting success, offspring production, and adult mortality. We then calculated the yearly per capita contribution to the metapopulation, a measure for sources or sinks (Runge, Runge & Nichols 2006), of meadows and monocultures over the research period. Because we have estimated natal and adult breeding dispersal rate between the two habitats (Chapter 5), we were able to investigate the role of sinks on metapopulation dynamics. Additionally, we validated our demographic estimates by comparing the yearly predicted population sizes with independent field counts. We calculated which parameters contributed most to the metapopulation, using a life-stage simulation analysis (Wisdom, Mills & Doak 2000).
MATERIALS & METHODS

Study area
The study was carried out between 2007 and 2013 in one of the core breeding areas of black-tailed godwits in the Netherlands, in southwest Friesland (52°55'N, 5º25'E), on 8480 ha of agricultural land. The study area was divided by polders, hydrological entities of which some of them are reclaimed from former lakes, and the polders by fields. The 2284 fields measured an average of 3.6 ha (SD = 2.3, range 0.3 – 17.4 ha). Per field, we classified grassland habitat on the basis of herb-richness and the occurrence of foot drains (small drainage channels which are 10-30 cm deep) into two types which accurately summarized the intensity of modern agricultural management (Chapter 2). Herb-rich meadows (20% of the study area) contained diverse grass and herb species and had groundwater tables no more than 30 cm below surface, while grassland monocultures (69% of the study area) had lower water tables, consisted dominantly of reseeded high-productive ryegrasses (Lolium sp.) and had underground drainage instead of foot drains. The remainder consisted of arable fields, mostly used for growing corn (Zea mays). Half of the study area is part of an agri-environmental scheme, with nest-protection (nests are protected from agricultural activities with no management restriction otherwise) as the most common measure (50%) (Table 1.2 in Chapter 1). The majority of herb-rich meadows is part of higher-level agri-environmental schemes, or managed by nature organisations. The patches consisting herb-rich meadows were on average 46 ha (range 1.3 – 657 ha). Black-tailed godwits are migratory and present in the study area from early March until mid-July (Gill et al. 2008; Hooijmeijer et al. 2013). In 2009, there were around 900 breeding pairs in our study area, of which 40% were breeding in monocultures (Chapter 2).

Data collection

COUNTS
We counted the number of individual black-tailed godwits on all fields in the years 2008-2013, except in 2011 (due to a lack of resources), on a weekly basis starting from the arrival period (± 15 March) until the early incubation phase (± 25 April). Thereafter, the grass would have grown too high to see all birds, and we would have missed the birds that started incubation. We did not count around noon, because during this time of the day most godwits were resting on roost sites. We excluded flocks of non-territorial godwits, as these were partially migrant black-tailed godwits of the islandica subspecies (Alves et al. 2012, personal observations of colour marked godwits). Some polders were not counted in some weeks, and in two years the grassy marshland area next to the Workumerwaard polder bordering Lake IJsselmeer was not counted at all. We had to exclude this subarea of 121 ha.

NESTS
Nests were searched and locations of nests measured by GPS. We used the egg flotation method (Liebezeit et al. 2007) to age the nest and predict hatching date, which happens ±
25 days after laying the first egg. The nests were revisited just before hatching, and we
returned every other day until hatching or depredation. A nest had hatched if there was at
least one chick in the nest, or if we found broken eggs without blood or yolk and
membranes clearly visible, or tiny egg fractions in the bottom of the nest. A nest was
considered unsuccessful if we found abandoned eggs that were not in the laying phase,
egg remains with blood or yolk, or an empty nest without any remains of eggs. See
Chapter 3 for more details.

MARKING
Adult godwits were captured on the nest with funnel shaped walk-in traps, remotely
controlled fall-traps, mist nets held horizontally above the nest, or by hand at the end of
the incubation stage (see also Schroeder et al. 2008). Adults were uniquely marked with
four plastic colour rings and one coloured flag, and a numbered metal ring. Chicks were
marked in the nest with a metal ring, and from 2008 onwards also with a plastic flag
engraved with a unique code. Chicks older than ten days that were captured in the field
were given the same markings as the adults, as from this age onwards the legs of the
chicks were large enough to fit a full colour ring combination. In recaptured chicks the
engraved leg flags were replaced, because colour ring combinations were easier to read
from a distance. See Chapter 4 for more details.

Sightings of marked individuals in subsequent years were used to calculate apparent
survival probabilities. For colour marked godwits we used sightings in the Netherlands
between 1 March and 31 July, the pre-breeding, breeding and post-breeding periods.
Adult godwits are unlikely to disperse outside the study area (Chapter 5), thus apparent
survival will approximate true survival. Besides, after the breeding phase before depar-
ture to their wintering area, many godwits use our study area to fuel up, thus the few
godwits that might have been missed during breeding would have a chance to be sighted
then. To limit mistakes in sightings, colour marked godwits must have been seen at least
twice during the season on different dates or by different observers. For the analysis of
godwits with engraved leg flags we included sightings during their migration.

Metapopulation Analyses
In our analyses of the contribution of different habitats to the metapopulation we chose to
model the combined demography of all meadow patches together as a single patch and all
monocultures as the alternative patch. Separate patches would have to low sample sizes
for robust analyses. We used the basis of the formula of Runge et al. (2006) to calculate if
the subpopulation was a source or a sink:

\[
C^r = q^{rr}_{Ad} + \sum_{s \neq r} q^{rr}_{Ad} + \beta^r \left( \sum_{s \neq r} q^{rs}_{Ad} + \sum_{s \neq r} q^{rs}_{Jf} \right)
\]

where \( r \) stands for the focal population and \( s \) for all the other populations, \( \phi \) stands for
apparent survival probability, \( \beta \) for the fecundity (number of young born per female), \( Ad \)
for adults and \( J \) for juveniles. The metric \( C^r \) is the per capita contribution of a member of
the focal population to the metapopulation, which differs from often used local population
growth rates ($\lambda$) by also taking emigrants into account. However, if survival probabilities are estimated in such a way that they equal true survival probability, and assuming that dispersal has no effect on survival, the formula can be modified as such:

$$C^r = S^r_{Ad} + \beta^r S^r_{J}$$

where $S$ stands for true survival. If $C^r > 1$ more individuals are contributed to the metapopulation than it loses to mortality and the population is a source, while if $C^r < 1$ the population is a sink. It is possible to add an age structure, which was necessary for our case as not all godwits started breeding in their second-calendar year (Chapter 5). We calculated the $C^r$ per year and an average $C^r$ over the study period.

To incorporate sampling errors of the measured demographic variables, we used a bootstrap approach to draw 10,000 random samples from the distributions of the survival and other fecundity estimates (see Table 6.1 and Table 6.2 for samples sizes and estimates calculated in this article and previous articles), with which we calculated mean, SE and 95% confidence intervals of the $C^r$. We used the beta distribution for proportions.

**Survival analyses**

Survival probabilities of young and adult godwits were estimated from resightings of marked individuals in subsequent years, with mark-recapture models in the program MARK (White & Burnham 1999). We ran separate analyses for chicks ringed in the nest with engraved leg flags and chicks and adults ringed with a colour mark combination, as different a priori model sets were used. For both sets we used two-year age class models, as survival and resighting rates may differ for individuals in their second-calendar year (2CY) and later in life.

We previously described a strong effect of habitat on the survival of chicks ringed with engraved flags in the nest; chicks born on monocultures had a lower survival (Chapter 4). Due to more years in which we could resight the birds since that study, we were now able to analyse if first year survival was year dependent. We compared models where resighting probability was constant over years, and where resighting probability could differ per year, as interaction or as additive effect for the 2CY and adult class. We kept the survival probability of the adult age class constant across years, to prevent overparameterization.

For the older chicks and adults marked with colour-ring combinations we compared models where both first-year survival and adult survival may differ per year or be constant. Moreover, first-year survival may differ between the two habitats, while adult survival has been shown to be independent of breeding habitat (Chapter 5). Resighting probability was modelled to be constant over years or different per year as interaction or as additive way for the 2CY and adult class. Because we also needed averaged demographic values over all study years to calculate the average $C^r$ per habitat type, we used the variance component analysis to estimate an average survival over the research period, with its accompanied SE (Burnham & White 2002), when survival probabilities differed per year.
We corrected for the bias emerged from the chicks we recaptured and whose engraved leg flags were changed into colour-ringed combinations, and were removed from the engraved leg flag database. This may underestimate first year survival, as those older chicks are the ones with higher survival probability. For this purpose, we estimated how many of the recaptured chicks would have survived based on the survival probability of older chicks, and calculated an unbiased survival by dividing the total number of chicks that would have survived by the total number of chicks ringed in the nest, as done in Chapter 4. As SE for the unbiased chick survival, we used the fraction of SE/estimate of the first year survival probability for chicks with engraved leg flags.

Because for both analyses the global model was not the fullest possible model, goodness-of-fit was tested with the median c-hat test integrated in program MARK. For the analysis with chicks with an engraved leg flag, we found no evidence for overdispersion as the \(\hat{c}\) was estimated 1.00 (± 0.01 SE), while for the analysis of the individuals marked with colour-ring combinations we used a \(\hat{c}\) of 1.77 (± 0.03 SE), both based on 100 iterations, to correct for a slight overdispersion of the data. We used Akaike’s Information Criterion corrected for small sample size (AICc) for the chicks marked with an engraved leg flag and corrected for overdispersion (QAICc) for the individuals marked with a colour-ring combination, for model selection and inference (Burnham & Anderson 2002).

**Fecundity**

The fecundity, or number of young produced per female, is calculated with the formula

\[
\beta = \text{nest success} \times \text{nr eggs hatched per successful nest} \times \left[1 + \text{renest} \times (1-\text{nest success}) \right] \times \text{proportion females}
\]

Because not all nests were found immediately during laying or after the clutch of usually four eggs was complete, nest success would lead to an overestimation if losses in the meantime would not be taken into account (Mayfield 1961). To account for this bias we estimated daily nest survival rates, the daily probability that a nest survived. Additionally, nests early in the incubation period have a lower daily survival rate than nests that are almost hatching (Chapter 3). Therefore, not correcting for nest age would yield an overestimation of hatching success. To calculate nest survival for nests laid on meadows and monocultures between 2007 and 2012, we modelled daily nest survival rates in MARK with nest age as covariate, and included the factors habitat and year, and the interaction habitat × year, which was shown to be important (see Chapter 3 for more details on the analysis). We did not correct for the existing seasonal difference in daily survival rate, because this variation needed to be included in the parameter estimates of nest survival. To calculate the percentage successful nests per grassland type per year, we used the product of the daily nest survival from 1 to 25 days old. With the deltamethod (Powell 2007) we calculated its accompanied SE. Because this method did not work for averaging nest success over the years of the study period, we simply averaged the nest successes per year as well as the SE’s.

Due to partial predation and unfertile eggs, not every egg in a successful nest hatches. With an \(\chi^2\)-test we compared if the number of hatched eggs per successful nest deviated between meadows and monocultures. We bootstrapped the number of successful hatched
eggs from our empirical sample for the analysis of sources and sinks, because the distribution was not normal.

The probability to lay a nest after nest failure is common in ground-breeding waders (Pakanen et al. 2013), as well as in godwits (van Balen 1959; Hegyi & Sasvari 1998; Schekkerman & Müskens 2000). In our research area, in a subpopulation breeding in the Haanmeer, a herb-rich polder, co-workers were able to estimate the probability to renest for the years 2013–2014 (Senner et al. submitted) as 0.20 (± 0.06 SE) (N = 51). This is a lower probability than the one of 0.41 (± 0.10 SE) (N = 22), found by Schekkerman & Müskens (2000), although the two estimates are not significantly different. Because of the low sample sizes of both studies, we combined their estimates in an assumed renesting probability of 0.26 (± 0.05 SE). Sex ratio did not significantly differ from 1:1 (Trimbos et al. 2013), thus we used 0.5 as proportion females.

Black-tailed godwits have been described to start breeding at different ages, and part of the 2CY individuals may stay at the African wintering grounds or staging areas in southern Europe (Cramp et al. 1983; Márquez-Ferrando et al. 2011). To calculate the proportion of 2CY individuals recruiting as breeder, one could divide the resighting probability of 2CY birds with the resighting probability of adults (>2CY). However, this method assumes that all resighted individuals would breed, and that individuals of different age-classes would have a similar probability to be resighted given that they returned to breed. Both assumptions are violated in our analysis, because some 2CY individuals return to the breeding area as prospectors, and young godwits have a higher probability to breed outside the research area (Chapter 5). As an approximation, we averaged the resighting probability of individuals with colour marks seen with territorial behaviour from Chapter 5, and the resighting rates of individuals ringed as older chicks with a colour-ring combination, of which the first estimate would underestimate the proportion 2CY breeders as dispersers are not seen territorial, and the second would lead to an overestimation as prospectors are also taken into account. Because our estimates are inaccurate, we used a wide SE of 10% of the estimation.

**LIFE STAGE SIMULATION ANALYSIS**

We performed a life-stage simulation analysis (LSA) to analyse the effect of the different demographic rates on \( C^r \), while considering the variation caused by process and sampling errors (Wisdom, Mills & Doak 2000). We used the same set of 10,000 iterations used for the bootstrap analysis for the total study period, for meadows and monocultures separately. For each demographic parameter we calculated the proportion explained variation (\( R^2 \)) in \( C^r \). We assumed no correlation between the demographic parameters, and thus included no covariance structure.

**POPULATION SIZE**

Counts often include noise, as some birds may be overlooked, while others were counted double. To account for this noise, we used a random effect model for Poisson data (Kéry & Schaub 2012). Moreover, to estimate the number of godwits for the polders where we were unable to count in some weeks, and to be able to calculate a confidence interval
around the week totals for the whole research area per year, we used a generalized random effect model in a Bayesian framework.

We used the following model, with random site and random week effects:

\[ C_{ij} \sim \text{Poisson}(\lambda_{ij}) \]

\[ \log(\lambda_{ij}) = \mu + \alpha_j + \epsilon_i \]

\[ \alpha_j \sim \text{Normal}(0, \sigma^2_j) \]

\[ \epsilon_i \sim \text{Normal}(0, \sigma^2_\epsilon) \]

where C is the count data which consists of counts per polder, separated for meadows and monocultures if a polder consisted of both grassland types, \( \lambda \) is the predicted count, \( \mu \) is the overall mean, and \( \alpha \) and \( \epsilon \) the random terms for site (j) and week (i) respectively.

From this analysis we derived total godwit counts per week for the whole study area, and separately for meadows and for monocultures. We used the maximum count per year as number of breeding pairs in that year. To calculate the posterior distributions of the parameters, counts per week for the meadows, monocultures and total research area, we used MCMC simulations implemented in program JAGS (Plummer 2003) that we executed from R (R Development Core Team 2011) with package R2jags. We defined the priors to be uninformative. We ran the MCMC algorithm with 20,000 iterations, burned the first 6000 and thinned the remainder to 1 in every 6 iterations. Convergence of the MCMC chains happened quickly and the Rhat, the measure of convergence, was one and therefore confirmed convergence.

**Predicted Population Size**

With the estimated demographic parameters it was possible to predict the yearly number of breeding godwits in our study area. We constructed a two-population projection matrix in which we included natal and adult dispersal estimates between meadows and monocultures (Chapter 5), see Appendix 6A. The dispersal estimates for young are: from meadows to monocultures 0.16 (± 0.06 SE), from monocultures to meadows 0.58 (± 0.12 SE). For adults they are: from meadows to monocultures 0.04 (± 0.01 SE), from monocultures to meadows 0.24 (± 0.03 SE). To investigate the effects of dispersal on the metapopulation, we also predicted population size when dispersal was set to zero.

**RESULTS**

**Survival analyses**

On monocultures the survival probability from nestling to 2CY was about 50% lower than on meadows (Table 6.1, monocultures: 0.05 (± 0.03 SE); meadows: 0.11 (± 0.03 SE); these are averages over all years based on chicks ringed with engraved flags in the nest). We found variation in first year survival for chicks ringed with engraved flags between years and habitats (and their interaction Table 6.1): in some years the difference between habitat types was especially great (2008-2010) whereas in other years first year survival was similar (2011–12). For model selection results, see Appendix 6B. The dataset on first year survival of the older chicks that got a full colour-ring combination (>10 d old) also
showed a difference between the habitat types (meadows 0.54 ± 0.06 SE, monocultures 0.36 ± 0.07 SE, Table 6.1), but did not show variation among the years. For model selection see Appendix 6B. Note that because of the high mortality of young chicks, this survival is considerably higher than of the chicks ringed as nestlings with engraved flags. After correcting for the bias caused by replacing leg flags by colour-ring combinations of pre-fledged chicks, probabilities for the first year survival of godwits were, on average, 0.13 for chicks born on meadows, and 0.06 for chicks born on monocultures (Table 6.1).

Adult survival probability estimated from the dataset of chicks ringed with an engraved flag was estimated as 0.87 (± 0.06 SE). This is similar to the average adult survival probability estimated with the dataset of birds marked with colour-rings (0.88 ± 0.02 SE) (Table 6.1). With this dataset we could also test for yearly variation in adult survival probabilities, which existed (Table 6.1). Adult survival probability was highest from 2012 to 2013 (0.97 ± 0.03) and lowest from 2008 to 2009 (0.81 ± 0.03 SE).

Table 6.1 Demographic parameters, with estimate and SE, which were used in the analysis to calculate $C'$. The sample sizes are the numbers marked with colour-ring combinations or with engraved leg flags.

<table>
<thead>
<tr>
<th></th>
<th>Meadows</th>
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<th>Monocultures</th>
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<td>SE</td>
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</tr>
<tr>
<td>First-year 2009</td>
<td>0.122</td>
<td>0.024*</td>
<td></td>
<td>0.030</td>
<td>0.030*</td>
</tr>
<tr>
<td>First-year 2010</td>
<td>0.242</td>
<td>0.032*</td>
<td></td>
<td>0.142</td>
<td>0.037*</td>
</tr>
<tr>
<td>First-year 2011</td>
<td>0.071</td>
<td>0.029*</td>
<td></td>
<td>0.070</td>
<td>0.048*</td>
</tr>
<tr>
<td>First-year 2012</td>
<td>0.076</td>
<td>0.030*</td>
<td></td>
<td>0.092</td>
<td>0.044*</td>
</tr>
<tr>
<td>Fraction 2 cy breeding</td>
<td>0.34</td>
<td>0.03***</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* used similar SE percentage of small chicks estimates
** because of zero SE for small chicks, we used percentage SE of chicks 2008–2012
*** we used a SE of 10%
The average resighting probability of a second calendar year bird marked with engraved flags was 0.34 (± 0.07 SE), and with a colour mark combination was 0.34 (± 0.05 SE). The resighting probability of adult birds with engraved leg flags was 0.44 (± 0.07 SE) and of adult birds with colour-ring combinations was 0.82 (± 0.01 SE). With the resighting probabilities found here and those from Chapter 5, we estimated that 34% of the godwits started breeding in their second calendar year.

**Fecundity**

Daily nest survival rates increased during the incubation period ($\beta = 0.028, \pm SE = 0.007$), and differed between grassland management type and between years. Nest success ranged between 21% and 69%, and in most years it was lower on monocultures than on meadows. On average, 54% (± 4 SE) of the nests hatched on meadows and 41% (± 6 SE) on monocultures (Table 6.2). The average number of eggs that hatched in a successful nest was 3.70 (range 2–5), which did not differ between nests laid on meadows and on monocultures ($\chi^2 = 4.85, df = 2, P = 0.11$). After including the chance to make a second clutch after failure, we estimated that on meadows on average 1.12 (± 0.19 SE) chicks hatched per pair and on monocultures hatched on average 0.87 (± 0.17 SE) chicks per pair.

**Sources and sinks**

The contribution to the metapopulation ($C'$) of birds breeding on meadows ($C_{\text{meadow}}$) during our study period was 1.01 (± 0.04 SE) which is not different from 1 (the 95% CI overlapping 1). Of the bootstrap results, 42% was lower than 1, which corresponds with the chance that the population breeding on meadows was a sink instead of a source.

<table>
<thead>
<tr>
<th>Table 6.2</th>
<th>Demographic parameters, with estimate and SE and N which were used in the analysis to calculate fecundity.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Meadows</strong></td>
<td>Estimate</td>
</tr>
<tr>
<td>Nest success 2007</td>
<td>0.418</td>
</tr>
<tr>
<td>Nest success 2008</td>
<td>0.687</td>
</tr>
<tr>
<td>Nest success 2009</td>
<td>0.531</td>
</tr>
<tr>
<td>Nest success 2010</td>
<td>0.503</td>
</tr>
<tr>
<td>Nest success 2011</td>
<td>0.509</td>
</tr>
<tr>
<td>Nest success 2012</td>
<td>0.605</td>
</tr>
<tr>
<td>Nest survival 2007-2012</td>
<td>0.542</td>
</tr>
<tr>
<td>Number eggs per successful nest</td>
<td>3.73</td>
</tr>
<tr>
<td>Chance renesting after failure</td>
<td>0.26</td>
</tr>
</tbody>
</table>

* SE derived by averaging the logit scale SE’s of all the years
** We could not test for differences between meadows and monocultures, thus the sample size is the total sample size.
the population breeding on monocultures, the $C_{\text{mono}}^r = 0.94$ (± 0.03 SE), with a 4% chance that the population was a source.

Because some demographic parameters differed between years, we could calculate a $C^r$ that varied over time (Fig. 6.1). On meadows, in three of the five years the population had a $C^r > 1$: 2009 had a 72% chance that the population on meadows was a source, 2010 it had a chance of 91% and 2012 a chance of 92% to be a source. In 2008 the meadow population had 28% of the bootstrap estimates higher than one, and thus had a higher chance to be a sink than a source, and in 2011 the population on meadows was most likely a sink, as only 2% of the bootstrap estimates exceeded one. The black-tailed godwit population breeding on monocultures had only in 2012 a $C_{\text{mono}}^r > 1$, with 92% of the bootstrap estimates higher than one. In 2008 and 2009 the population was a sink, with <1% of the bootstrap results higher than one and in 2010 and 2011 most likely a sink with 30% and 11% respectively higher than one.

**Life stage simulation analysis**

The results of the LSA showed that survival of the first year had the greatest effect on the $C^r$, followed by adult survival, for both populations on meadows (Fig. 6.2) and monocultures (Fig. 6.3). The proportion replacement clutches and 2CY individuals starting to breed did not contribute ($R^2 < 0.01$), and nest success only a little ($R^2 = 0.03$). The number of chicks per hatched nest had a greater effect on $C_{\text{meadow}}^r$ ($R^2 = 0.20$) than on $C_{\text{mono}}^r$ ($R^2 = 0.06$).
Comparison of real and predicted population size

Between 2008 and 2013, the total number of godwit pairs breeding in our study area declined from ± 990 to ± 830 pairs (Fig. 6.4). The decline was not linear, as there was an increase by ~100 pairs from 2012 to 2013. The population on meadows fluctuated around a mean of 520 pairs on ca. 1700 ha (density: 0.31 pairs/ha), while the population on monocultures first decreased from 430 pairs in 2008 to 270 pairs in 2010, and grew in 2013 until 330 pairs on ca. 5850 ha (densities in 2008: 0.07, 2010: 0.05, and 2013: 0.06 pairs/ha). The growth differed between meadows and monocultures mainly from 2009 to 2010, when an increase of godwits pairs was found on meadows and a decrease of pairs on monocultures.

The population growth calculated on the basis of our estimated demographic variables (Fig. 6.5A) strongly resembled the population growth based on the counts (Fig. 6.4): the population on meadows maintained their numbers between 2007 and 2013, whereas monocultures showed a slight decrease in numbers until 2012, followed by an increase. Although the sample size is rather low, the correlation between predicted total number of
pairs and total counted number of pairs was significant (Pearson’s correlation: $r = 0.99$, $t = 10.39$, $df = 3$, $P < 0.01$), as well as for the pairs on monocultures ($r = 0.96$, $t = 6.04$, $df = 3$, $P < 0.01$). The correlation between predicted and counted number of pairs on meadows was not significant at the 5% level, although the correlation coefficient was high ($r = 0.80$, $t = 2.31$, $df = 3$, $P = 0.10$).

To visualise the effects of dispersal on population growth, we restricted dispersal in the metapopulation model to zero. The population breeding on meadows would grow slowly, and the population on monocultures would decrease in absence of dispersal (Fig. 6.5B).
DISCUSSION

In our multi-year in depth demographic study of a large metapopulation of black-tailed godwits, we showed that traditional herb-rich agricultural meadows, often especially managed for breeding birds, tend to be a source habitat for godwits, as they are intended to be. We also showed that modern agricultural grassland monocultures on average acted as a sink. In addition, we showed that the strength of the sources and sinks varied between years, that meadows could be sinks, and that monocultures could be sources in some years. The life-stage simulation analysis suggested that the variation in growth rates...
between years was mainly explained by fluctuations in adult and first-year survival. We were able to validate the demographic variables by comparing ‘real’ population growth (based upon counts made during the pre-breeding phase), with a predicted population growth (based upon the calculated demographic estimates). Even though we could not take into account factors such as the number of emi- and immigrants to and from outside our study population and yearly differences in dispersal rates, real and predicted growth rate estimates were very similar. The finding that when we restricted dispersal in the model to zero (Fig. 6.5B), the population on meadows showed a stronger increase and the population on monocultures a stronger decrease, is evidence that dispersal from meadows to monocultures prevented an increase in population size on meadows.

**Spatial population dynamics**

Dispersal between populations is considered as an important driver for population dynamics (Greenwood & Harvey 1982; Hanski 1998; Bowler & Benton 2005; Beissinger et al. 2006). In absence of dispersal, the godwit population breeding on meadows would grow until its (unknown) carrying capacity, and because the population on monocultures would go extinct with an averaged $C^*$ of 0.94, the size of the metapopulation would become similar to the carrying capacity of the meadow habitat. However, dispersal prevented the growth of meadow population, suggesting a ‘leakage’ of birds to sinks. Without dispersal the population breeding on monocultures would eventually go extinct, but immigration appears to prevent this.

That the population on meadows was rather stable may suggest that carrying capacity is reached. However, numbers of breeding pairs have been at least twice as high in the past. For example, the Haanmeer (a herb-rich meadow area in our study area of 130 ha) between 2008-2012 supported ~100 godwit breeding pairs, while in the years 1985–1997 there were on average ~200 pairs (S. Bakker, Staasbosbeheer, pers. comm.). Furthermore, it is often assumed that young animals would suffer more from intraspecific competition, and thus would not be able to occupy a territory in high-quality habitat if carrying capacity is reached (Greenwood & Harvey 1982; Bowler & Benton 2005). Yet, young godwits were as able as older birds to settle in high density breeding areas (Chapter 5). In fact, density may also have positive effects if godwits are attracted by the presence of other godwits (Allee effect) (Soutullo et al. 2006). In view of the small variation in numbers over the period of study the role of density-dependence, an important regulator of populations (Watkinson & Sutherland 1995; Ratikainen et al. 2008), has been beyond even correlative investigation.

The rate of dispersal from monocultures to meadows (58% for young and 16% for adults) was higher than the other way around (16% for young and 4% for adults) (Chapter 5). Some individuals, mainly young, perceive this habitat as good enough to try and reproduce. Yet, as monocultures were not preferred over meadows, they cannot be considered an ‘ecological trap’ (Delibes, Ferreras & Gaona 2001; Battin 2004; Gilroy & Sutherland 2007). However, as in absolute numbers more individuals dispersed from meadows to monocultures (because of the low productivity of chicks), monocultures were a form of ‘attractive sink’ (Delibes, Gaona & Ferreras 2001).
Coinciding with an increased productivity on monocultures in 2011 and 2012, from 2012 to 2013 the population of our study area grew remarkably. Indeed, nest survival and chick survival on monocultures were highest in these last two years. Fewer nests were situated on fields that were mown during the incubation period (Chapter 3) and we noticed a change in attitude of the farmers. This change of attitude may be the result of the presence of our research team, which led to an increase of local knowledge of meadow bird conservation, encouraged the finding and protecting of godwit nests and chicks, and led to an overall higher motivation of the farmers to protect wildlife. Interestingly, however, the population trend at the national level also showed stabilisation from 2009 onwards (Boele et al. 2013) (Figure 2 in Box A). Although the conservation case for meadowbirds has been heralded both at the national level (efforts of Vogelbescherming Nederland) and at the provincial level (e.g. www.keningfanegreide.nl), it seems a little farfetched that the change in attitudes would exerted itself nationally. Monitoring demography of godwits on both meadows and monocultures remain necessary to assess whether this trend continues.

The importance of demographic analysis versus counts to assess habitat quality
Habitat quality in heterogeneous landscapes is often determined by comparisons of local population trends (e.g. Oosterveld et al. 2011; Perkins et al. 2011). However, in source-sink systems where sinks are supported by sources, the suitability of sinks can be overestimated (Kleijn et al. 2011b), especially when individuals select poor habitats over high quality habitats (Johnson 2007), a phenomenon which primarily happens in human-altered landscapes (Battin 2004). Accordingly, to understand how variation in habitat affects population dynamics it is necessary to treat habitat quality and habitat attractiveness as separate properties (Kristan 2003). If, in our study system, we only had looked at population trends on meadows and monocultures, we would have concluded that the two would not differ much in habitat quality, and consequently that agri-environmental schemes of the highest-level commonly applied on meadows would barely be more effective than the low-level schemes on monocultures. Our demographic analysis suggests otherwise.

Relevance for meadowbird management practices
We have shown here that in wet herb-rich meadows black-tailed godwits achieved higher productivity than in the modern standard for agricultural grasslands, i.e. monocultures. Although we used the term ‘wet herb-rich meadows’, this habitat type encompass more than just more herbs (Chapter 2): it is often especially managed for birds with the highest-level agri-environmental schemes. This means that the groundwater level is higher, the vegetation consists of more structure, and that mowing is delayed until after the nesting phase of the birds. The majority of grassland monocultures in our study area also incorporates agri-environmental schemes, but of the lowest level. Low-level schemes require that nests should be spared during mowing (by leaving a large patch of grass around the nest) (Musters et al. 2001), but intensive land use is otherwise possible.

Even though black-tailed godwits breeding on meadows contributed on average to the metapopulation, the question arises whether a $C_r$ of 1.01 is high enough to ensure a future
for this species. Within our study period of five years, meadows have been a sink in one year (2011) and stable ($C^r \approx 1$) in another. To overcome environmental and demographic stochasticity (Lande 1993), aiming for a higher $C^r$ is necessary. What should be done? The LSA showed that of all demographic parameters, increasing first-year survival would be the most effective, followed by increasing adult survival. Mowing on herb-rich meadows is now often delayed until after the nesting phase (Chapter 3), but mowing tends to happen before the chicks actually fledge. Delaying mowing until after the chick rearing phase would likely increase chick survival on meadows. In addition, for chicks hatching on monocultures the distance to herb-rich meadows where they have enough to eat and where there is cover (Chapter 4), should be adequate, and the route of passage not obstructed by, for instance, steep ditches and high traffic roads. Protecting key foraging sites during the migration route is important for adult survival (Piersma 2002; Hooijmeijer et al. 2013).

Another measure would be to prevent 'leakage' from meadows to monocultures. Fragment size may affect dispersal (Bowler & Benton 2005), as smaller patches are related to higher emigration and immigration rates (Crone, Doak & Pokki 2001). This higher dispersal rate would suggest that from small source habitats more (young) birds would disappear, and 'leak' to sink habitat. Increasing the size of meadow areas may be beneficial, but the relationship between patch and dispersal ought to be further investigated. Nevertheless, larger fragment sizes of herb-rich source habitat may also positively influence their success (Fahrig 2003), as smaller sized fragments are more prone to disturbance, for instance, by disturbance from road traffic and human presence, which both negatively influence breeding densities (Reijnen, Foppen & Meeuwsen 1996; Holm & Laursen 2009).

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APPENDIX 6A. Population estimates in meadows and monocultures using demographic parameters.

In order to estimate the number of breeding Black-tailed Godwits in meadows and monocultures our study area, we used the temporal estimates of the demographic parameters from this study (Table 6.1 and 6.2) and the dispersal estimates from Chapter 5. We implemented this in an age structured spatial matrix population model (ref Hunter & Caswell 2005), written as \( N(t+1) = A t N t \). The age-structured projection matrix is defined as:

\[
A_t = \begin{bmatrix}
\beta_{2cy,1,t} & \beta_{ad,1,t} & 0 & 0 & 0 \\
0 & 0 & (1-f_{j1})S_{j1,t} & 0 & 0 \\
0 & f_{ad,1}S_{ad,t} & f_{ad,1}S_{ad,t} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
0 & (1-f_{j2})S_{j2,t} & (1-f_{ad2})S_{ad,t} & 0 & 0 \\
0 & (1-f_{ad2})S_{ad,t} & (1-f_{ad2})S_{ad,t} & 0 & 0 \\
\end{bmatrix}
\]

where \( \beta \) stands for the fecundity of second calendar years (2cy) or adults (ad) in meadows (1) or monocultures (2) at time \( t \), \( f \) is the site fidelity (which is 1 - dispersal) between their first and second year (\( j \) for juveniles) or older (\( ad \) for adults), and \( S \) stands for survival. We could not differentiate between dispersal probabilities between their 2cy and 3cy and adult dispersal probability, and we could not distinguish in differences between years (hence the lacking \( t \)). Moreover, we could not differentiate between survival probabilities of 2cy and 3cy and adults and adult survival does not differ between meadows and monocultures (Chapter 5).

As stage vector \( N_t \) we used:

\[
N_t = \begin{bmatrix}
N_{1cy,1} \\
N_{2cy,1} \\
N_{ad,1} \\
N_{1cy,2} \\
N_{2cy,2} \\
N_{ad,2} \\
\end{bmatrix}
\]

we calculated the stable stage structure of the population. We used the number of breeding pairs counted in 2008 on meadows (560) and monocultures (430) and calculated with the stable stage structure how many adults, 2CY and 1CY the population existed of, considering that 0.34 of the 2CY birds started breeding, and used this as starting population size \( (N, t_0 = 2008) \). As starting breeding population size we used the number of breeding pairs on meadows (560) and monocultures (430) counted in 2008. Calculations were performed in program R (version 2.14.0, R Development Core Team 2011).
APPENDIX 6B. Model selection results for nest survival, first-year survival and adult survival.

Table 6B.1  Model results of yearly survival analysis of black-tailed godwit chicks marked in the nest with an engraved flag. Apparent survival is φ, and resighting probability is p. The term hab means that there is an effect of where the chicks are born: meadows or monocultures, time means that the survival or resighting probability is year dependent, add denotes when the effects are additive between age classes. We included an age structure of 2 years (a2). Adult survival was kept constant. The best model was the one where first year survival had an interaction between habitat and time. The resighting probability was time dependent, with an additive effect for adults. Parameter estimates are given in the main text of the article.

<table>
<thead>
<tr>
<th>Model</th>
<th>npar</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Weight</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>φ(a2-hab*time/.).p(a2-time/time-add)</td>
<td>17</td>
<td>1511.030</td>
<td>0.000</td>
<td>0.843</td>
<td>60.620</td>
</tr>
<tr>
<td>φ(a2-hab*time/.).p(a2-time/time)</td>
<td>20</td>
<td>1514.389</td>
<td>3.359</td>
<td>0.157</td>
<td>57.856</td>
</tr>
<tr>
<td>φ(a2-hab/.).p(a2-time/time)</td>
<td>13</td>
<td>1542.265</td>
<td>31.235</td>
<td>0.000</td>
<td>99.989</td>
</tr>
<tr>
<td>φ(a2-hab*time/.).p(a2-time/time-add)</td>
<td>9</td>
<td>1546.477</td>
<td>35.447</td>
<td>0.000</td>
<td>112.299</td>
</tr>
<tr>
<td>φ(a2-hab/.).p(a2-./.)</td>
<td>5</td>
<td>1556.568</td>
<td>45.538</td>
<td>0.000</td>
<td>130.454</td>
</tr>
<tr>
<td>φ(a2-hab*time/.).p(a2-./.)</td>
<td>13</td>
<td>1561.931</td>
<td>50.901</td>
<td>0.000</td>
<td>119.654</td>
</tr>
</tbody>
</table>
Table 6B.2  Model results of yearly survival analysis of black-tailed godwit chicks older than 10 days and adults marked with a colour mark combination. Apparent survival is $\phi$, and resighting probability is $p$. The term $hab$ means that there is an effect of where the chicks are born: meadows or monocultures, time means that the survival or resighting probability is year dependent, $add$ denotes when the effects are additive between age classes. We included an age structure of 2 years (a2). We did not include an effect of habitat for adult survival.

<table>
<thead>
<tr>
<th>Model</th>
<th>npar</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Weight</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi_{(a2-hab/time)}p_{(a2-./.)}$</td>
<td>10</td>
<td>2580.201</td>
<td>0.000</td>
<td>0.354</td>
<td>374.987</td>
</tr>
<tr>
<td>$\phi_{(a2-.time)}p_{(a2-./.)}$</td>
<td>9</td>
<td>2581.892</td>
<td>1.690</td>
<td>0.152</td>
<td>378.692</td>
</tr>
<tr>
<td>$\phi_{(a2-hab/.)}p_{(a2-time/time)}$</td>
<td>15</td>
<td>2582.655</td>
<td>2.454</td>
<td>0.152</td>
<td>376.349</td>
</tr>
<tr>
<td>$\phi_{(a2-hab/.)}p_{(a2-time/time-add)}$</td>
<td>10</td>
<td>2583.090</td>
<td>2.889</td>
<td>0.084</td>
<td>377.876</td>
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<tr>
<td>$\phi_{(a2-hab/time)}p_{(a2-time/time)}$</td>
<td>19</td>
<td>2583.633</td>
<td>3.431</td>
<td>0.064</td>
<td>360.228</td>
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<td>$\phi_{(a2-hab/time)}p_{(a2-time/time-add)}$</td>
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<td>2583.914</td>
<td>3.713</td>
<td>0.055</td>
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</tr>
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<td>$\phi_{(a2-.time)}p_{(a2-time)}$</td>
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<td>2584.788</td>
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<td>$\phi_{(a2-.time)}p_{(a2-time)}$</td>
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<td>2585.290</td>
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</tr>
<tr>
<td>$\phi_{(a2-time/time-add)}p_{(a2-.time)}$</td>
<td>14</td>
<td>2585.674</td>
<td>5.472</td>
<td>0.023</td>
<td>372.389</td>
</tr>
<tr>
<td>$\phi_{(a2-time/time)}p_{(a2-time)}$</td>
<td>9</td>
<td>2585.861</td>
<td>5.660</td>
<td>0.021</td>
<td>362.661</td>
</tr>
<tr>
<td>$\phi_{(a2-time/time-add)}p_{(a2-time)}$</td>
<td>19</td>
<td>2587.335</td>
<td>7.134</td>
<td>0.010</td>
<td>363.931</td>
</tr>
<tr>
<td>$\phi_{(a2-time/time-0)}p_{(a2-time/time-add)}$</td>
<td>14</td>
<td>2588.039</td>
<td>7.383</td>
<td>0.007</td>
<td>374.755</td>
</tr>
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<td>$\phi_{(a2-time/time)}p_{(a2-time)}$</td>
<td>14</td>
<td>2588.454</td>
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</tr>
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<td>$\phi_{(a2-time/time-add)}p_{(a2-time)}$</td>
<td>14</td>
<td>2589.262</td>
<td>9.060</td>
<td>0.004</td>
<td>375.977</td>
</tr>
<tr>
<td>$\phi_{(a2-hab/.)}p_{(a2-.time)}$</td>
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<td>2589.463</td>
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<td>0.003</td>
<td>394.306</td>
</tr>
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<td>2589.823</td>
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<td>0.003</td>
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<td>$\phi_{(a2-.time)}p_{(a2-.time)}$</td>
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<td>0.001</td>
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<td>$\phi_{(a2-time/time)}p_{(a2-time/time-add)}$</td>
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<td>2591.843</td>
<td>11.642</td>
<td>0.001</td>
<td>368.439</td>
</tr>
<tr>
<td>$\phi_{(a2-time/.)}p_{(a2-time)}$</td>
<td>23</td>
<td>2593.705</td>
<td>13.503</td>
<td>0.000</td>
<td>362.178</td>
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<td>$\phi_{(a2-time/time)}p_{(a2-.time)}$</td>
<td>20</td>
<td>2594.335</td>
<td>14.134</td>
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<td>368.902</td>
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<td>$\phi_{(a2-time/time)}p_{(a2-time)}$</td>
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<td>2594.485</td>
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<td>$\phi_{(a2-time/time-add)}p_{(a2-time)}$</td>
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<td>2594.641</td>
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<td>$\phi_{(a2-time/.)}p_{(a2-time/time-add)}$</td>
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<td>18.015</td>
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<td>2604.055</td>
<td>23.853</td>
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