Combined effects of waggle dance communication and landscape heterogeneity on nectar and pollen uptake in honey bee colonies

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The instructive component of waggle dance communication has been shown to increase resource uptake of *Apis mellifera* colonies in highly heterogeneous resource environments, but an assessment of its relevance in temperate landscapes with different levels of resource heterogeneity is currently lacking. We hypothesized that the advertisement of resource locations via dance communication would be most relevant in highly heterogeneous landscapes with large spatial variation of floral resources.

To test our hypothesis, we placed 24 *Apis mellifera* colonies with either disrupted or unimpaired instructive component of dance communication in eight Central European agricultural landscapes that differed in heterogeneity and resource availability. We monitored colony weight change and pollen harvest as measure of foraging success.

Dance disruption did not significantly alter colony weight change, but decreased pollen harvest compared to the communicating colonies by 40%. There was no general effect of resource availability on nectar or pollen foraging success, but the effect of landscape heterogeneity on nectar uptake was stronger when resource availability was high. In contrast to our hypothesis, the effects of disrupted bee communication on nectar and pollen foraging success were not stronger in landscapes with heterogeneous compared to homogenous resource environments.

Our results indicate that in temperate regions intra-colonial communication of resource locations benefits pollen foraging more than nectar foraging, irrespective of landscape heterogeneity. We conclude that the so far largely unexplored role of dance communication in pollen foraging requires further consideration as pollen is a crucial resource for colony development and health.
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Abstract

The instructive component of waggle dance communication has been shown to increase resource uptake of *Apis mellifera* colonies in highly heterogeneous resource environments, but an assessment of its relevance in temperate landscapes with different levels of resource heterogeneity is currently lacking. We hypothesized that the advertisement of resource locations via dance communication would be most relevant in highly heterogeneous landscapes with large spatial variation of floral resources.

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Our results indicate that in temperate regions intra-colonial communication of resource locations benefits pollen foraging more than nectar foraging, irrespective of landscape heterogeneity. We conclude that the so far largely unexplored role of dance communication in pollen foraging requires further consideration as pollen is a crucial resource for colony development and health.
Communication is a key feature in social insect colonies, and allows them to allocate the colony’s work force effectively to necessary tasks at hand (Hölldobler & Wilson 2009; Seeley 1995; Wilson 1971). An example of this is the recruitment for collaborative foraging, where successful scouts guide idle or unsuccessful nest mates to valuable resource locations (Biesmeijer & de Vries 2001; Dechaume-Moncharmont et al. 2005; Seeley 1983). The honey bee waggle dance found in the genus *Apis* is a unique, highly sophisticated and well-studied recruiting behaviour. Honey bees are also capable of spreading information about the resource environment via dance-independent behaviours, e.g. by offering samples of gathered nectar to nest mates via trophallaxis (Farina et al. 2005; Grüter et al. 2006). The waggle dance, however, does not only provide a motivational component that includes information about the presence and identity of rewarding resources. It also includes the well-known instructive component (Menzel et al. 2011; von Frisch 1967). A dancing forager communicates the distance and flight angle relative to the sun’s current azimuth, and hence the relatively precise spatial position of a rewarding food source (von Frisch 1967).

Studies on the western honey bee (*A. mellifera* L.) revealed that waggle dances are highly efficient in recruiting foragers to artificial food sources (Sherman & Visscher 2002; von Frisch 1967) and enable honey bee colonies to concentrate their foraging efforts to the most rewarding resources (Schmickl & Crailsheim 2004; Seeley 1986; Seeley 1995; Seeley et al. 1991).

Continuous information exchange about variable resource patches could increase resource uptake rates of honey bee colonies significantly (Donaldson-Matasci & Dornhaus 2012), and provide fitness advantages (Brown 1988; Dyer 2010; Seeley & Visscher 1988). Dance communication might also allow for selective pollen foraging by allocating the colony worker force to preferred
pollen sources (Danner et al. 2016), which enables more consistent exploitation of high-quality resources (Donaldson-Matasci & Dornhaus 2014). Pollen quality may differ significantly between plant species (Haydak 1970), and pollen quality and diversity are important factors for honey bee health (Alaux et al. 2017; Alaux et al. 2010; Di Pasquale et al. 2016; Di Pasquale et al. 2013).

Nevertheless, the importance of dance communication for an efficient use of nectar or pollen resources in agricultural landscapes is still unclear. Benefits of spatial information conveyed by the instructive component of waggle dancing for colony fitness were found to be highly dependent on resource density, quality and distribution (Donaldson-Matasci & Dornhaus 2012; Donaldson-Matasci & Dornhaus 2014; Dornhaus & Chittka 1999; Dornhaus & Chittka 2004; Dornhaus et al. 2006; Okada et al. 2012; Sherman & Visscher 2002). Dornhaus & Chittka (2004) were able to show a significant effect of dance communication on resource uptake in a complex tropical environment. However, there were no detectable benefits of the instructive component of dance communication in human-modified temperate regions, where distribution of resource patches was less complex (Dornhaus & Chittka 2004). Within a temperate landscape the benefit of dance communication may change with shifting resource conditions over the seasons (Sherman & Visscher 2002). Landscapes may differ in the number, proportion and spatial arrangement of different habitat types (Tscharntke et al. 2005), which affects resource distributions. Human-modified temperate landscapes are often dominated by intensively used arable land (Benton et al. 2003; Robinson & Sutherland 2002). They are characterized by few large habitat patches (Tscharntke et al. 2005), including mass-flowering crops that provide plenty of easily available resources (Holzschuh et al. 2016; Westphal et al. 2003). Such areas have low landscape heterogeneity and form simple resource environments, with easy to find resource
patches. This can reduce the value of instructive information exchange between foragers (Beekman & Lew 2008). In addition, landscapes may contain varying amounts of semi-natural habitats for which pollen foragers show a strong preference (Danner et al. 2016; Steffan-Dewenter & Kuhn 2003; Steffan-Dewenter et al. 2002). Semi-natural habitats increase the complexity of a resource environment by generating a more heterogeneous landscape. Here mean patch sizes are more variable and generally smaller (Beekman & Ratnieks 2000; Steffan-Dewenter et al. 2002). Increased heterogeneity and decreased patch size raise the value of instructive information exchange among honey bee foragers (Beekman & Lew 2008). Accordingly, the dance frequency of honey bee foragers increases with higher proportion of semi-natural habitats (Steffan-Dewenter and Kuhn 2003).

The design of previous studies may have obscured some beneficial effects of waggle dance communication (Schürch & Grüter 2014). Honey bee colonies in previous studies remained at the same location during the whole experimentation time. This means that foragers were able to gather and exchange information about resources during phases when communication was not disturbed (Sherman and Visscher 2002; Dornhaus and Chittka 2004b; Donaldson-Matasci and Dornhaus 2012; Donaldson-Matasci et al. 2013) and were probably able to profit from this information while dance communication was disrupted.

The aim of our study was to investigate the importance of the information about resource locations conveyed by honey bee dance communication for nectar and pollen foraging success of colonies exposed to landscapes with varying resource heterogeneity. We experimentally disrupted the instructive component of dance communication in honey bee colonies and measured nectar and pollen uptake rates. Unlike previous studies, we performed this in a number of spatially separated human-modified temperate landscapes featuring a variety of levels of
complexity and resource availability. For the first time in this context, we used landscape heterogeneity, i.e. heterogeneity in the spatial arrangement of resource patches within a landscape, which describes the complexity of the resource environment on the landscape level and independently from the amount of available resources. We expected that the value of dance communication for colony performance would increase with decreasing resource availability and increasing landscape heterogeneity.

Material and Methods

Study region

The study was conducted in Central Europe, in the vicinity of Würzburg, Germany. Within the study region, simple landscapes, dominated by intensive agriculture, and complex landscapes with a mixture of arable land, woodland, hedgerows, meadows and settlements can be delineated. In order to assess the role of waggle dance communication in different resource environments we selected eight circular landscapes (distances among landscapes ranged from 5.0 to 31.2 km) with differing proportions of intensively used arable land and semi-natural habitats (Tab. 1). Landscapes were analysed within a radius of 2 km (1265.64 ha area), because mean bee foraging distances under comparable circumstances were shown to lie well within this range (Steffan-Dewenter & Kuhn 2003), and more than 90% of pollen foraging recruitments advertise patches within this distance to the colony (Danner et al. 2014). The experiment took place in late summer 2013 (18th July – 18th August 2013).

Landscape-level floral resource availability and heterogeneity
Resource availability in each of the eight study landscapes was assessed in two steps. Firstly, we distinguished between habitats that provided noteworthy plant resources for honey bees and those that were unlikely to be utilized for foraging. Resource providing habitats were hedgerows, intensively or extensively used grassland, fallows, meadow orchards, maize fields, sunflower fields, legume fields (including alfalfa, white and red clover and legume mixtures) and non-flowering crop fields (predominantly weeds in beet and cereal fields and vineyards). The relative cover of each habitat type was computed using a geographical information system (Arc-GIS) and digital land use data, which was validated by field inspections. Secondly, we estimated total flower cover on the 2000m scale. For this purpose, flower cover was assessed in at least three randomly selected 100m² plots in each habitat type that provided measurable amounts of resources (Scheper et al. 2015). Total flower cover was extrapolated by summing estimations of mean flower cover per area multiplied by the relative cover of each habitat type across all habitat types in each landscape. In order to keep track of changes in resource distributions over time, the assessment of the flower cover was done twice. The two discrete timespans for which flower cover was assessed in this study were named period A and period B. Period A lasted from 17th July to 2nd August 2013, while vegetation period B lasted from 3rd August to 18th August 2013. Mean patch size of resource-providing habitats, a configurational measure of landscape complexity, was used as proxy for resource heterogeneity in the landscape. Heterogeneous and more complex resource environments are characterized by small mean patch sizes. Flower cover (resource availability) and mean patch size (landscape heterogeneity) were not correlated significantly ($r = -0.30; t = -1.16, df = 14, p = 0.265$).

Study organism
Twenty-four colonies of *Apis mellifera carnica* were established on 11\textsuperscript{th} July 2013 by making nucleus colonies that were equal in size. Each colony was provided with three fully occupied brood combs, two food combs (Zander measure) and a mated queen. All queens were sister-queens from a professional breeder (Schüler, Münster, Germany). Nucleus colonies were inserted into hive boxes with nine frames. The empty space was filled with two empty combs and two wax sheet frames. Sets of three honey bee colonies were placed in the centre of each study landscape on individual levelled tables.

**Disruption of waggle dance communication**

The hive box design enabled us to disrupt the instructive component of waggle dance communication using a method following the established approach of Sherman & Visscher (2002) and Dornhaus & Chittka (2004). The hive boxes were placed on levelled tables, and rotation of hives by 90\textdegree allowed for combs to be positioned horizontally, preventing bees from orienting their dances in a specific angle to the gravitational cue. All incoming foragers in rotated hives were forced to enter the hive box via the top frame next to the window, to encourage them to dance there (Dornhaus & Chittka 2004). Combs were held in place by a tight-fitting slot system that prevented tilting while hive boxes were rotated. In a dark hive without additional cues, dances are performed in random directions and no longer provide consistent spatial information about resource locations (Dornhaus & Chittka 2004; Sherman & Visscher 2002; von Frisch 1967). The successful disruption of waggle dance orientation on horizontal combs in our experimental hive boxes was confirmed by in-hive video recordings (Fig. S1). Dance orientation on horizontal combs can be re-established if dancers are allowed to see the sun, blue sky or any directional light source (Sherman & Visscher 2002; von Frisch 1967). As an additional treatment
we attempted to restore dance orientation by providing a directional light source in form of a
closable circular window of 2.5 cm in diameter. However, dance observations revealed that
dance orientation could not be fully restored (Fig S1). Therefore, we do not report results of this
treatment.

We analysed groups of colonies with (1) disrupted communication: combs were positioned
horizontally and dances were disoriented, in order to investigate the impact of disrupted dance
communication; and (2) intact communication: combs were positioned vertically in a dark hive,
allowing for unimpaired dances.

All sets of three colonies were moved between the eight landscapes every fourth day during
night time. This was repeated seven times, so that each set of colonies was placed in each of the
eight landscapes for four days by the end of the experiment. For the statistical analysis each four-
day period was regarded as a distinct time step. All communication treatments were randomly re-
assigned to the three colonies in each landscape at each time step. All 24 colonies were tested in
each treatment and landscape. Minimum distance between consecutive colony locations was ten
kilometres to prevent foragers from returning to former colony sites (mean = 19.2 km, $SD = \pm 6.9$
km). At the same time, this procedure reduced the value of information about the resource
environment that was previously acquired by foragers. This prevented carry-over effects from
masking the influence of waggle dance communication on resource uptake. The spatial
arrangement of resource patches and of landmarks that could guide workers during foraging
flights differed considerably between landscapes. Foragers were shown to perform waggle
dances advertising resource patches in up to 4.4 km distance on the first day after moving to a
new environment (Danner et al. 2014). Due to the methodology, it was not possible to record
data on colonies blindly.
**Colony development**

The presence of the marked queen and brood in the colonies was confirmed every eight days and the total brood area was estimated. In one colony a queen had to be replaced by a reserve sister queen, because she died in the course of the experiment. Data obtained from this colony were not excluded from the presented models, as excluding data did not significantly change model outcomes.

**Colony weight**

Colony weight change is supposed to reflect resource uptake on colony level. Nectar is the main factor influencing colony weight changes on a daily basis (Meikle et al. 2008; Seeley 1995). A portable platform balance (Kern EOB35K10) was used to weigh the colonies. Each colony was weighed at the beginning of the experiment and on the first and fourth day at each site. Weighing took place during night time, when all foragers were back in their nest and there was no further resource uptake.

**Pollen uptake**

The complete pollen forage of each colony was sampled throughout the first day that colonies spent in a new landscape. A total of 192 pollen samples was collected. The pollen was gathered using pollen traps with removable perforated plates (5 mm diameter holes) in front of the colony entrance (Keller et al. 2005). Pollen traps were activated during night time after moving the colonies. Deactivation and pollen collection occurred during the consecutive night, following the weighing of colonies.
The pollen samples were stored in a -20°C freezer. Later on, pollen samples were vacuum-dried, cleaned from insect parts and other artefacts and weighed to the nearest 0.01 g using a lab scale (Kern Type 430-33). Mean weight-loss (± se) by vacuum drying was 17.5% ± 1.3%.

Statistics
We used linear mixed-effects models in R version 3.2.0 (R Core Team 2015) with the package lme4 (Bates et al. 2014) to test for effects of instructive dance communication, flower cover and mean patch size, as well as respective interactions, on colony weight change and dry-weight of pollen harvest. Effects on colony weight change were only tested during times when pollen traps were not active. Identity of colony, site and time step were included as random factors in each model to address pseudo-replication and design imbalances. P-values, degrees of freedom and F-values were obtained using the R-package lmerTest using the Satterthwaite approximation for degrees of freedom (Kuznetsova et al. 2015). Minimum adequate models were identified using ANOVA-tests. P-values of factors that were not included in the minimum adequate models but that were relevant for the hypotheses were calculated by adding the respective factor to the minimum adequate model. As integral part of the main hypothesis, the effects of communication treatments on dependent variables were always shown in the figures, regardless of statistical significance. Data on pollen dry-weight were cubic-root transformed to meet the assumption of normal distribution for linear models. Model residuals were visually inspected for spatial autocorrelation and violation of assumptions of normality and homoscedasticity. See Tab. 2 for an overview of tested factors and interactions.

Results
Effects of dance communication on foraging success

Mean daily colony weight changes did not differ significantly between colonies with disrupted or intact dance communication (Fig. 1; see Tab. 2 for statistics). Due to the scarcity of floral resources in late summer in the region of Lower Franconia, Germany, all colonies lost weight over the study period and during most time steps (mean weight change = -37.87 g/day, $se = \pm 6.04$ g/day, $n = 192$; Fig. 1).

Rotating the combs to a horizontal position and thereby disrupting dance communication significantly reduced the dry-weight of pollen harvest by 40.25% (Fig. 2; Tab. 2).

Effects of flower cover and mean patch size

Mean flower cover of habitat types ranged from 0 – 85.2 % (mean = 8.4 %; $se = \pm 1.6$ %). The flower cover in the studied landscapes varied considerably, both among the eight landscapes and between the two distinct mapping periods (Tab.1). In every landscape and during each mapping period we recorded highly rewarding patches of nectar-providing crops like sunflower and legume fields, flower-rich areas promoted by agri-environmental schemes, or flower-rich grasslands. Overall there was no significant effect of flower cover on colony weight change (Fig 3; Tab. 2) or dry-weight of pollen harvest (Fig. 4; Tab. 2).

We used mean patch size in a landscape to define landscape heterogeneity (see Tab.1 for patch size range), with higher mean patch size in landscapes with lower heterogeneity. Mean patch size was significantly positively correlated with colony weight change (Fig. 5; Tab. 2) and dry-weight of pollen harvest (Fig. 6; Tab. 2). Additionally, flower cover affected the impact of mean patch size on colony weight change, with stronger effects of mean patch size when flower cover was high (Fig. 7; Tab. 2).
There was no significant interaction between flower cover or mean patch size of the studied landscapes and the effect of dance communication on foraging success (Fig. 3 – 6; Tab. 2).

Discussion

In this study we analysed the interplay between the instructive component of dance communication and landscape structure, with regard to colony foraging success. Contrary to our hypothesis, we found that honey bee communication about locations of rewarding floral resources did not promote the nectar intake of bee colonies in temperate agricultural landscapes.

The amount of pollen collected in colonies within hives that were rotated in order to disrupt dance orientation was reduced by 40%, indicating an important role of instructive communication in pollen foraging. Our data reveal that the amount of brood reared by a colony which is a main driver of pollen foraging activity was not affected by hive rotations (Fig S2) but we cannot exclude that the horizontal comb position has further unknown effects on brood rearing behaviour or pollen foraging and storage. Landscape heterogeneity affected nectar and pollen foraging success, but in contrast to our expectation, the benefits of instructive dance communication were not modulated by the complexity of the resource environment. Resource availability within the tested landscapes had no direct effects on nectar or pollen foraging success, but altered effects of landscape heterogeneity on nectar foraging success.

It is important to keep in mind that we, and others, disrupted only the instructive information in waggle dance recruitment behaviour. Waggle dances also include information about the presence of rewarding nectar or pollen sources, as well as about their identity (von Frisch 1967; von Frisch 1968). Dancing foragers are also known to activate idle foragers as well as to reactivate experienced but currently unemployed foragers (Grüter & Farina 2009), so that dancing
generally increases forager recruitment (Gilley 2014; von Frisch 1968). Thus dancing can have a positive effect on resource uptake rates that is unrelated to communication of resource location directions.

In our study, colony weight change was not impacted by manipulation of dance communication, although we deliberately placed colonies in experimentally selected environments where effective communication should offer advantages for foraging success. We tested a number of different landscapes that varied significantly in resource availability and heterogeneity. The study was conducted during late summer, when resources in the study region were generally scarce and colonies lost in weight, but some resource-rich patches were still available and information exchange was expected to be valuable (Okada et al. 2012; Sherman & Visscher 2002). Additionally, repeatedly moving the colonies to a new environment created an exceptionally short-living resource environment. This forced foragers to repeatedly update information about locations of profitable resources instead of making good use of previously acquired information, which might have masked effects in earlier experiments (Schürch & Grüter 2014). In contrast to our hypothesis the high temporal turnover and the spatial heterogeneity of resource patches experienced by foragers did not increase the importance of communication. In temperate landscapes the instructive component of waggle dance communication might only prove to be advantageous for nectar foraging in environments under very specific conditions, like strong intra- or interspecific competition (Donaldson-Matasci & Dornhaus 2012; Seeley & Visscher 1988) or during specific seasonal resource distributions (Sherman & Visscher 2002). While the conditions were deliberately chosen in order to identify the specific conditions under which communication of resource location would be beneficial, it is important to note that these conditions are not representative for the whole flowering period. In
early spring, for example, resources would also be scarce but possibly much more patchily
distributed in form of few flowering trees and scrubs, which may increase the value of
directional dance communication. Additionally, if instructive dance communication does only
outweigh dancing costs if advertised resources can be used over extended time periods (Schürch
& Grüter 2014), repeatedly moving colonies every four days prevented us from identifying these
long-term benefits. This should be addressed in future field experiments. Contrary to our
findings in nectar foraging, our data show that the disruption of instructive dance communication
had a strong negative effect on pollen foraging. To our knowledge, only two related studies also
investigated the effect of instructive dance communication directly on pollen forage instead of
colony weight change (Donaldson-Matasci & Dornhaus 2012; Donaldson-Matasci & Dornhaus
2014). However, the studies were restricted to Sonoran Desert scrub and grassland habitats. In
these non-temperate landscapes dance communication increased pollen uptake rates
independently of resource availability, but only if resource distribution was patchy. Additionally,
instructive dance communication also proved to be advantageous, depending on resource
conditions (Donaldson-Matasci & Dornhaus 2012). Due to the study design foragers could make
use of information on resource locations gathered before communication was disrupted (Schürch
& Grüter 2014) or ignore available dance information in favour of previously acquired
information on resource locations (Grüter & Ratnieks 2011). Therefore, these studies possibly
failed to reveal the actual extent of the effect of dance communication. As colonies in our study
were moved to unknown landscapes with considerably different spatial features at the same time
at which treatments in individual colonies were changed, we prevented that foragers profited
from previously acquired information on resource locations. This allowed us to assess the total
benefits of directional dance information under the given conditions. Our findings for temperate
landscapes under the conditions of sub-optimal resource availability do not support the
hypothesis that resource distribution affects the value of directed dance communication in honey
bee colonies. It remains to be confirmed if this is also true when foragers can profit from the
directional dance information for a longer period of time, as we only investigated effects on
short-term benefits. The fact that in the tested temperate landscapes dance communication
always improved pollen foraging, but never nectar foraging, is remarkable. We suspect that this
is related to the circumstance that honey bee colonies exploit a higher diversity of plant species
for pollen than for nectar (Requier et al. 2015). The identity and diversity of pollen sources may
have a strong effect on colony health (Alaux et al. 2010; Di Pasquale et al. 2016; Di Pasquale et
al. 2013). Dance communication may allow for a selective and diverse but still effective pollen
foraging, but may be less important for effective nectar foraging in temperate landscapes. In fact,
it was shown that waggle dance communication affects the composition of pollen forage
(Donaldson-Matasci & Dornhaus 2014). A mechanistic explanation for the differences in our
findings between nectar and pollen foraging might be, that pollen foragers are more motivated to
follow dances and make use of the instructive component of the dances, e.g. of scouts that
advertise novel resource patches. It has been shown that previous experience in the field and in-
hive olfactory information affect the way foragers deal with available dance information (Farina
et al. 2012). In addition, pollen foragers were shown to have a preference for pollen collected
from plant species found in semi-natural habitats (Danner et al. 2016) which are generally
relatively small, scarce, patchily distributed and probably quickly depleted. Therefore pollen
foragers could profit more from the instructive component of dance communication than nectar
foragers that commonly forage in presumably more easy to find mass-flowering crop fields or
other floral resources with abundant nectar supply (Beekman & Lew 2008). Additionally, pollen
advertisement in plants can be more limited in time than nectar advertisement and pollen within inflorescences can be rapidly depleted (Herrera 1990; Stone et al. 1999). High ephemerality of pollen sources and possibly increased competition would increase the benefits of effective communication (Dornhaus & Chittka 2004; Seeley & Visscher 1988). We cannot rule out the possibility that additional factors affected pollen foraging activity, as disrupting dance communication coincided with hive rotation (Sherman & Visscher 2002). It could be argued that rotating the hives affected the brood, brood-provisioning behaviour or brood rearing activity which is known to be strongly correlated with pollen foraging activity (Al-Tikrity et al. 1972; Dreller & Tarpy 2000; Free 1967; Pankiw et al. 1998). While a small proportion of larvae may be malformed, brood rearing in general and egg-laying activity of queens are not known to be affected by horizontal comb position (Chauvin 1960). In our study the amount of reared brood seemed unaffected by comb position (Fig S2). We cannot exclude that other components of brood rearing activity are affected by hive rotation and further research on this might help to confirm that indeed disruption of the instructive dance communication caused the observed effects on pollen foraging. However, the random exchange of treatments every four days combined with a considerably longer development time of bee brood minimised possible effects of comb rotation on brood rearing. Although our treatment to control for effects of hive rotation by restoring directed dances on horizontal combs did not work, we therefore conclude that the measured effects of comb orientation on pollen foraging success were most probably due to the disrupted instructive dance information. Incoming pollen was only sampled during the first day within a new environment, in order not to disrupt protein supply and hence brood rearing. To which extent our findings can be extrapolated to longer time periods needs further investigation.
Studies on landscape-related foraging patterns of honey bee colonies are still rare (Couvillon et al. 2014; Danner et al. 2014; Danner et al. 2016; Härtel & Steffan-Dewenter 2014). In our study, variation in the generally low resource availability within late summer in temperate landscapes had no direct effect on foraging success. Irrespective of overall resource availability, foragers probably concentrated their efforts on few but most valuable resource patches. However, especially in the most resource rich landscapes, landscape heterogeneity had a strong effect on foraging success. Foraging was most successful in landscapes that contained flower-rich, large and easy to find resource patches, like mass-flowering crop fields. With increasing landscape heterogeneity, i.e. decreasing patch sizes, colony foraging success decreased. Foragers presumably spent less time within the smaller, quickly depleted patches (Cresswell & Osborne 2004) and hence probably more time on travelling between the scattered patches. This may reduce foraging efficiency (Westphal et al. 2006).

Conclusions

Although there is an increasing number of theoretical studies and field experiments addressing the possible benefits of the instructive component of waggle dance communication (Beekman & Lew 2008; Donaldson-Matasci et al. 2013; Donaldson-Matasci & Dornhaus 2012; Donaldson-Matasci & Dornhaus 2014; Dornhaus & Chittka 2004; Dornhaus et al. 2006; Okada et al. 2012; Schürch & Grüter 2014; Sherman & Visscher 2002), this study demonstrates that we still lack some essential knowledge regarding its actual relevance on colony level. Even in heterogeneous temperate landscapes and under specific conditions that were expected to increase the benefits of advertisement of resource locations, there were no short-term benefits of instructive dance communication for nectar foraging. In an unknown environment individual search abilities of
honey bee foragers and newly established knowledge of resource locations may be sufficient to
secure colony foraging success. It is possible that communicating nectar resource locations in
temperate landscapes will only provide benefits on the long-term (Schürch & Grüter 2014),
which was prevented in our study. Importantly, our data indicate that, within temperate
landscapes, waggle dancing plays a far more important role in pollen foraging than in nectar
foraging. As pollen is the major protein source in honey bee hives, dance communication can be
expected to have significant effects on colony development and health. This underpins the
potential evolutionary advantage of dance communication and suggests that future research
should focus more on pollen foraging ecology of honey bees.

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Landscape parameters of the eight selected landscapes for a 2000 m radius buffer around experimental colonies.

Flower cover is given for the two distinct mapping periods. Means ± standard errors and ranges.
| Landscape parameter                  | Mean ± se | Range    |
|-------------------------------------|-----------|----------|
| % Semi-natural habitat              | 7.8 ± 2.5 | 0.4 - 16.6 |
| % Arable land                       | 71.5 ± 5.7 | 51.1 - 89.6 |
| Flower cover - Period A [ha]        | 23.9 ± 2.9 | 11.1 - 33.3 |
| Flower cover - Period B [ha]        | 12.5 ± 3.2 | 3.4 - 26.0 |
| Mean patch size [ha]                | 1.5 ± 0.2  | 0.8 - 2.3  |
Table 2 (on next page)

Results of linear mixed effects models relating colony weight change and dry-weight of pollen harvest to explanatory variables.

\( n = 8 \) landscapes, \( n = 24 \) colonies, \( n = 127 \) colony weight measurements, \( n = 127 \) pollen samples.
| Explanatory variables                      | nDF | dDF  |   F   |   p   |
|-------------------------------------------|-----|------|-------|-------|
| **Colony weight change [g]**              |     |      |       |       |
| Communication                             | 1   | 111.93 | 1.03  | 0.312 |
| Flower cover                              | 1   | 125.84 | 2.64  | 0.107 |
| Mean patch size                           | 1   | 8.93   | 10.35 | 0.011 |
| Communication × flower cover               | 1   | 111.37 | 0.40  | 0.528 |
| Communication × mean patch size           | 1   | 111.43 | 0.01  | 0.924 |
| Flower cover × mean patch size            | 1   | 114.93 | 7.25  | < 0.001 |
| Communication × flower cover × mean patch | 1   | 111.11 | 0.39  | 0.532 |
| **Dry-weight of pollen harvest [g]**      |     |      |       |       |
| Communication                             | 1   | 111.99 | 11.02 | 0.001 |
| Flower cover                              | 1   | 107.25 | 0.52  | 0.473 |
| Mean patch size                           | 1   | 7.816  | 8.18  | 0.022 |
| Communication × flower cover               | 1   | 110.75 | 0.001 | 0.977 |
| Communication × mean patch size           | 1   | 110.32 | 1.28  | 0.260 |
| Flower cover × mean patch size            | 1   | 97.57  | 1.96  | 0.164 |
| Communication × flower cover × mean patch | 1   | 110.72 | 1.17  | 0.282 |

1 nDF: numerator degrees of freedom; dDF: denominator degrees of freedom
Figure 1

Effects of dance communication on mean daily weight change (± se) of honey bee colonies.

Disrupted: colonies with horizontal comb position and disoriented dances; and intact: colonies with non-affected dance communication on vertically positioned combs. ns: $p > 0.05$. 

![Figure 1 Image](image-url)
Figure 2

Effects of dance communication on mean dry-weight (± se) of pollen harvest collected by honey bee colonies.

For treatments see Fig. 1. ***: $p \leq 0.001$. 
Figure 3

The relationship between flower cover and mean daily weight change (± se) of honey bee colonies.

For statistics see Tab. 2.
Figure 4

The relationship between flower cover and mean dry-weight (± se) of pollen collected by honey bee colonies.

For statistics see Tab. 2.
Figure 5

The relationship between mean patch size and mean daily weight change (± se) of honey bee colonies.

Regression line fitted with linear model. For statistics see Tab. 2.
Figure 6

The effect of mean patch size within landscapes on mean dry-weight ($\pm se$) of pollen collected by honey bee colonies.

Regression line fitted with linear model. For statistics see Tab. 2.
Figure 7

The effect of mean patch size on mean daily weight change of honey bee colonies depending on flower cover within the landscape.

Grey area: 95% confidence interval. For statistics see Tab. 2.