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ARTICLE

Agroecosystems

Agroecological measures in meadows promote honey bee colony development and winter survival

Julie Hernandez[1,2,3] | **Yann-David Varennes**[3] | **Alexandre Aebi**[1,4] | **Vincent Dietemann**[2,5] | **André Kretzschmar**[6]

[1]Laboratory of Soil Biodiversity, Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland

[2]Swiss Bee Research Centre, Agroscope, Bern, Switzerland

[3]Fondation Rurale Interjurassienne (FRI), Courtételle, Switzerland

[4]Institute of Anthropology, University of Neuchâtel, Neuchâtel, Switzerland

[5]Department of Ecology and Evolution, Biophore, UNIL-Sorge, University of Lausanne, Lausanne, Switzerland

[6]INRAE, Unité Biostatistique et Processus Spatiaux, Site Agroparc, Avignon, France

Correspondence
Julie Hernandez
Email: julie.hernandez@unine.ch

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Abstract

The homogenization of agricultural landscapes has led to a decrease in pollinator diversity and abundance. In response to this decline, farmers have implemented agroecological measures, which, in meadows, aim at providing more floral resources. These measures are the availability of unmown floral strips, delayed mowing, and discouraging the use of the conditioner, a device known to harm insects. The aim of our study was to investigate the cascade of effects of these agroecological measures on honey bee colony development and winter survival. We (1) determined the effect of these measures on colony size during the nectar and pollen collecting season in spring and summer, (2) evaluated the effect of spring and summer colony sizes on autumn size, and (3) described the effect of colony size in autumn on winter mortality. In this study, 300 honey bee colonies were monitored over three years in three cantons of Switzerland. Colony size was defined by the numbers of brood cells and of adult workers. Honey bee colony size in summer and autumn was improved by agroecological measures on meadows and likely contributed to the increased overwintering success. This study is a first step toward the targeted identification of viable agroecological measures on temporary meadows that can be implemented to promote honey bee colonies health in the agricultural landscape.

KEYWORDS

agricultural landscapes, agri-environmental schemes, agroecological measures, *Apis mellifera*, colony size, honey bee, meadow management, winter colony losses

INTRODUCTION

In response to the negative effects of intensive agriculture on pollinators and on overall biodiversity, agri-environmental schemes have been implemented since the 1990s in most European countries (Albrecht et al., 2007; Marja et al., 2019; Uthes & Matzdorf, 2013; Zingg et al., 2019). A variety of agroecological measures aim at providing additional food and nesting resources for pollinators, as the ecological service they provide increases productivity (Ricketts et al., 2008). The specific effects of landscape composition and floral resources on honey bee development and winter losses have been demonstrated using large-scale monitoring studies

(Genersch et al., 2010; Kretzschmar et al., 2016; Kretzschmar & Frontero, 2017; Kuchling et al., 2018). The implementation of agroecological measures was shown to maintain diverse floral resources benefitting the development and survival of honey bee colonies during and after periods of scarcity (Alaux et al., 2017; Decourtye et al., 2010; Odoux et al., 2014; Requier et al., 2015; Wintermantel et al., 2019). Finding measures that can be implemented in meadows, and effectively benefit honey bees, is a major challenge as meadows are a crucial part of fodder in dairy and crop production regions across Europe (Huyghe et al., 2015).

The aim of our study was to identify, among a set of agroecological measures implemented by farmers in meadows, those effectively increasing floral resources to benefit honey bee health (Sutter et al., 2019). The measures considered were leaving unmown floral strips, delayed mowing, and foregoing the use of conditioner devices while mowing. The conditioner hastens the drying of grass after mowing, thereby improving hay quality, but is harmful to bees and other insects visiting the flowers during mowing (Fluri & Frick, 2002; Humbert et al., 2009). These studies on conditioners observed dead insects in the field during mowing operations, but the impact on bee colonies has not been documented.

We here tested the cascading effects of the implementation of these agroecological measures in proximity of the apiaries, in order to better understand the underlying mechanisms (Requier et al., 2017; Shakarian et al., 2015). This cascade included the effects of (1) the agroecological measures on colony size during spring and summer (June–July), at the time they are applied, (2) spring and summer colony size on autumn colony size, and (3) autumn colony size on winter mortality. For this, the size and winter survival of 300 honey bee colonies belonging to amateur beekeepers voluntarily participating in the study were monitored over three years at 30 apiaries. Two parameters of colony size were assessed: the number of adult bees and the number of capped brood cells from which young adults emerge. These parameters were chosen because they can respond differently to the agroecological measures (e.g., brood will not be affected directly by foregoing to the use of a conditioner when mowing, while adult honey bees will) and because their biological interdependence influences colony development and activity during nectar and pollen collecting season (Kretzschmar & Maisonnasse, 2022) as well as their survival over winter (Imdorf et al., 2010).

Winter survival of honey bee colonies is also strongly affected by the ectoparasitic mite *Varroa destructor* (Hernandez et al., 2022). We thus considered the effect of infestation rates of adult honey bee workers by this parasite in October, at the time when their impact on colony health is greatest (Hernandez et al., 2022). By identifying effective agroecological measures or combinations of such measures in meadows, our results allow for adjustment of meadow management to optimize honey bee colony health.

MATERIALS AND METHODS

Study sites and agroecological measures in meadows

The study was conducted over three successive years (from March 2018 to March 2021) and took place in the Cantons of Vaud, Jura, and Bern in western Switzerland. The agricultural landscape of these regions is characterized by a mosaic of diverse elements such as meadows, arable fields, and forests (Lachat et al., 2010). Legume plants (mainly white clover, red clover, and alfalfa) are important sources of nectar and pollen and are frequently found in meadows (Agroscope, 2021; Ziaja et al., 2018). The Swiss Agricultural Policy defines three types of meadows: temporary, permanent, and ecological (BLW, 2004). Temporary meadows are included in crop rotation and last up to five years before being replaced by crops, whereas permanent meadows last for several decades. These two meadow types receive fertilizer, are mowed two to five times per year, and are occasionally used as pastures. For both meadow types, farmers individually choose their harvest dates and equipment. In contrast, in ecological meadows, the Swiss Agricultural Policy sets the earliest mowing dates. Moreover, ecological meadows receive little or no fertilizer.

Thirty volunteer beekeepers managing apiaries in the three cantons were enrolled in the study. Recruitment occurred during information sessions and volunteer selection was based on the following criteria: age of beekeeper (<70), apiary size (≥10 colonies), and distance to another selected beekeeper's apiary (≥5 km). The colonies in selected apiaries had not been equalized for size at the beginning of the monitoring period and the queens heading them were mostly unrelated. Each monitored apiary marked the center of a 2-km-radius sector in which agroecological measures were considered to possibly affect the development and health of the colonies. The 2-km radius has been defined as an average foraging radius for honey bees (Steffan-Dewenter & Kuhn, 2003). Two sectors were located in canton Bern, eight in canton Jura, and 20 in canton Vaud (Figure 1). Five of the Vaud sectors extend into the neighboring canton of Fribourg. The total sector area was 1256 ha.

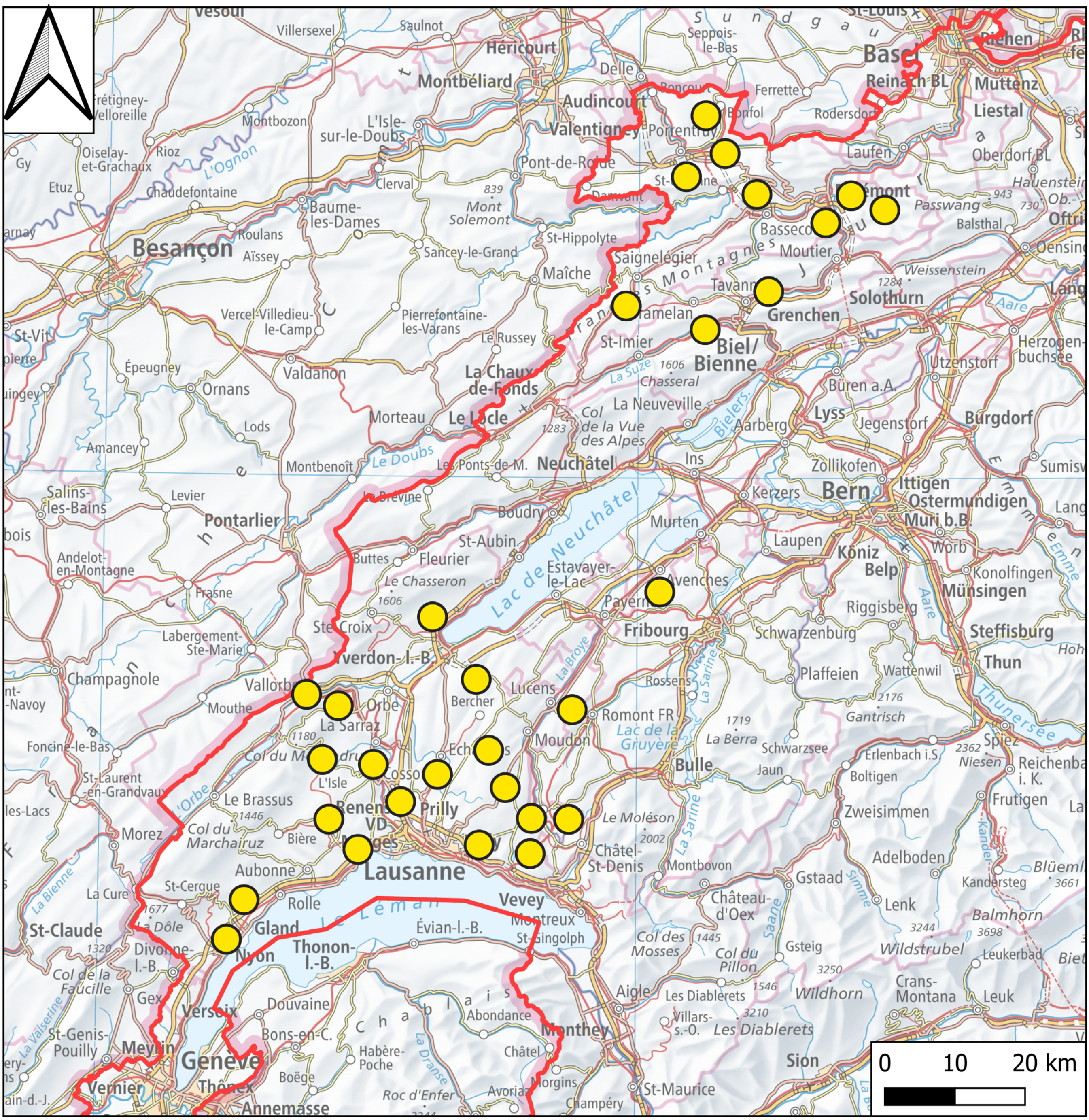

FIGURE 1 Locations (yellow dots) of the 30 monitoring sectors across western Switzerland.

Farmers owning meadows within the sectors were given the opportunity to apply agroecological measures that aimed at enhancing meadow exploitation by honey bees in return for subsidies. In temporary meadows, three measures were implemented, alone or in combination: (1) to forego conditioner use when mowing; (2) to leave a strip unmown during each of the mowing operations performed between June 1 to August 31 (time of legume, i.e., white clover, red clover and alfalfa, flowering); (3) to delay one mowing operation until legumes flowering ended. The combination of (2) + (3) was not considered as relevant because leaving an unmown strip in a late-mown meadow could produce hay with an insufficient quality for cattle feeding. In permanent meadows and ecological meadows, only foregoing to the use of a conditioner was proposed to the participants. The other measures were not relevant because ecological meadows already have specific rules regarding mowing dates, and because permanent meadows were assumed to have less legume flowers than temporary meadows.

On average, meadows represented ca. 300 ha (24% of total sector area; Table 1). Temporary and permanent meadows represented ca. 80% of meadows and were distributed across the landscape (see example in Figure 2).

Data collection

Landscape data

Landscape data originated from public sources. Data for forest and urban areas as well as bodies of water from 2019 were obtained from Cantonal services of geographic information (Geoportal SIT-Jura, Geoportal Canton de Berne, ASIT-VD catalogue). All agricultural land-use types were provided by Cantonal services of agriculture (Jura, Bern, Vaud, Fribourg). Agricultural data provided the following information: field location, field surface area, crop type, and whether agroecological measures had been implemented. These datasets were used to quantify the total surface area per land-use type, within the 2-km-radius sectors around the monitored apiaries. Maps of land use around apiaries were computed through QGIS (QGIS 3.16.1-Hannover).

Honey bee colonies and quantification of their size

Each of the 30 apiaries, containing 10 monitored colonies, was owned and managed by volunteer beekeepers following the local recommended practices (Apiservice, 2022). Beekeepers were allowed to split their colonies or adjust their size between April and June, after which they were instructed not to implement any measure that could interfere with our colony size assessment.

To assess the effects of agroecological measures implemented in meadows on honey bee colony size, the number of adult honey bees and capped brood cells in the colonies was quantified in June, July, and October. These three periods were chosen because June and July define the floral resource scarcity period (Requier et al., 2017) when agroecological measures are implemented, while colonies begin with winter preparations in October (Hernandez et al., 2022; Imdorf et al., 2010). The quantification of the two colony-size parameters was obtained using the ColEval method (Hernandez et al., 2020). Briefly, a calibrated estimation of the percentage of the comb surface area occupied by adult honey bees and by capped brood was performed and subsequently converted into number of adult individuals and brood cells. Adult workers and brood data for 2018 and 2019 were previously used in a study by Hernandez et al. (2022).

Measure of *V. destructor* infestation rates in October

For the assessment of *V. destructor* infestation rates during the October apiary visit, adult honey bee workers (mean = 300, SD = 50) were sampled from open brood

TABLE 1 List of meadow types, corresponding agroecological measures, surface area, and codes used in the analyses.

Meadow type	Agroecological measure description	Average surface area in hectares	Average % of total sector surface area	Code used in analyses
Temporary meadows	Temporary meadows without agroecological measures	96	7.6	TM.no.aems
	Mowing without conditioner	20	1.5	TM.no.cond
	Unmown floral strip	1.30	0.1	TM.strip
	Delayed mowing	4.86	0.3	TM.delay
	Combination of mowing without conditioner use and leaving an unmown floral strip	2.6	0.2	TM.no.cond.strip
	Combination of mowing without conditioner and delaying mowing	5.33	0.42	TM.no.cond.delay
Permanent meadows	Permanent meadows without agroecological measures	78.22	6.22	PM.no.aems
	Mowing without conditioner	21.8	1.73	PM.no.cond
Ecological meadows	Ecological meadow without agroecological measure	52.8	4.12	EM.no.aems
	Mowing without conditioner	8.14	0.65	EM.no.cond

Note: Numbers indicate the average surface area across sectors and years and the proportion of the total sector area occupied by each element. The last column indicates how each element was coded in the models presented in Appendix S1.

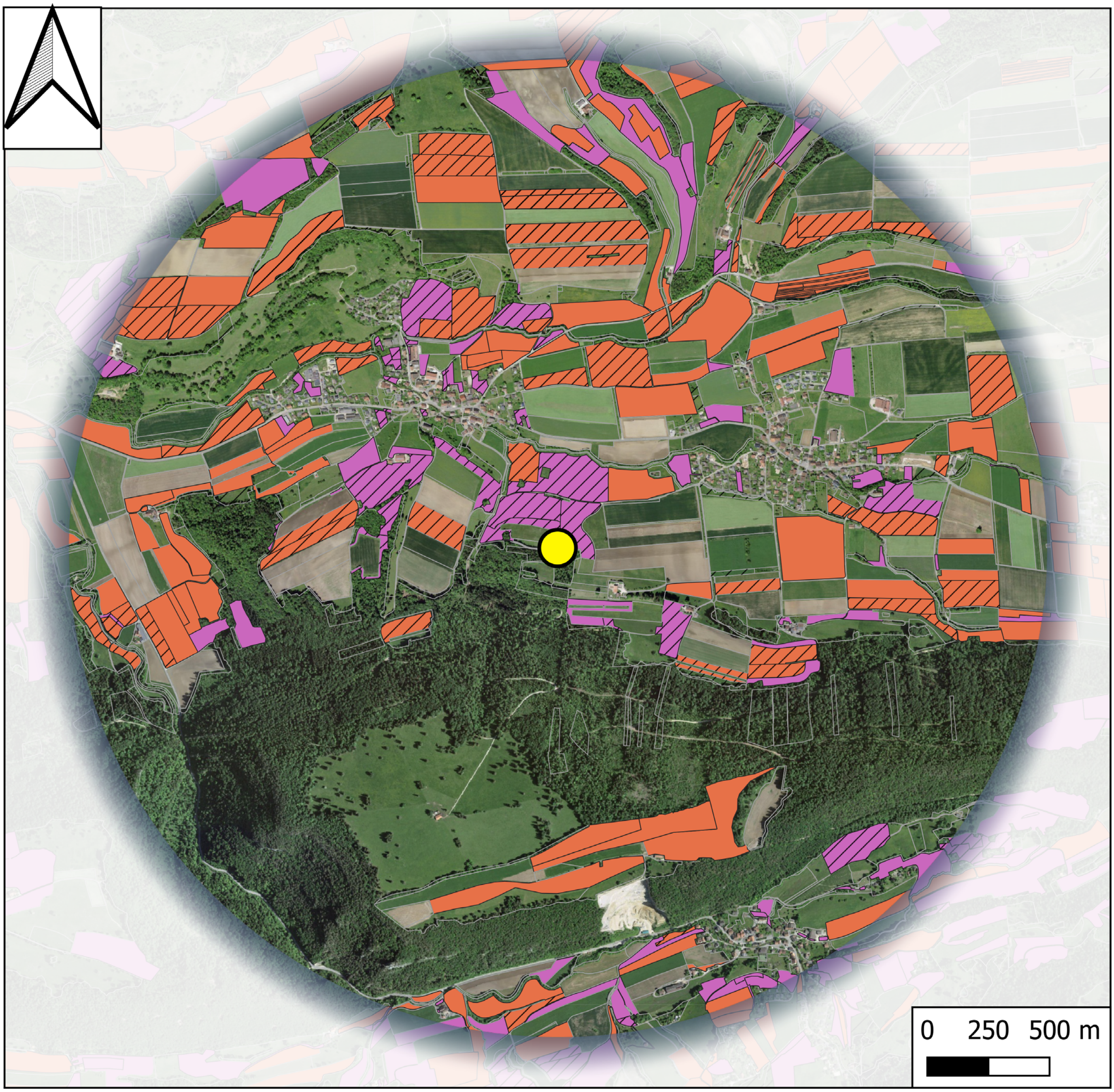

FIGURE 2 Example of one 2-km-radius study sector. Orange: temporary meadows; pink: permanent meadows. Dashes indicate meadows managed with agroecological measures as detailed in Table 1. Yellow dot: apiary location. Aerial photograph accessed via MapGeoAdmin-WMS on 3 March 2022.

combs of each colony. The samples were placed in a plastic zip bag, stored on ice, and brought to the laboratory where they were stored at −20°C until processing. During processing, each sample was first weighed to determine the number of adult honey bees they contained and then washed with soapy water following a standard protocol to dislodge mites for counting (Dietemann et al., 2013). From these data, the number of mites per 100 workers was calculated. The infestation rate data for 2018 and 2019 were previously used in a study by Hernandez et al. (2022).

Colony mortality

Colony mortality was recorded after the overwintering period, that is, at the beginning of April 2019, 2020, and 2021. Beekeepers replaced dead colonies each year with nuclei prepared in the spring of the previous season and attributed them new identification numbers.

Statistical analysis

Principal components analyses (PCAs, R package [ade4]; R Core Team, 2019) were used for selecting the meadow types (including those without agroecological measures) that contributed most to the differentiation of the landscape structure in the sectors around the apiaries. Variables that best correlated with the first two dimensions of the PCA identified meadow types for which the surface areas were variable enough for their effect on colonies to be tested statistically. This step was necessary because the implementation of measures in the field was not controlled but dependent on the decisions of farmers volunteering for the study. We included temporary meadows without measures in the analysis as baseline to disentangle the effect of the resources provided by the varying surface areas of meadows themselves, and that of the meadows subjected to agroecological measures. PCAs were run on the three years separately. Meadow types that contributed more than the average contribution of inertia (10%) of the first two eigenvalues were selected for model construction (Abdi & Williams, 2010). Generalized linear mixed models (GLMMs, R package [lme4]) with Gaussian distribution (with Identity as link function) were used to investigate the relationship between the highest contributing agroecological measures in meadows identified by PCA and honey bee colony size in June and July. The variable apiary was used as random effect. The same GLMM modeling method (Gaussian distribution, Identity as link function, and apiary as random effect) was applied to meadows without agroecological measures to identify a possible direct effect of meadows per se independently of the agroecological measure implemented. The effect of summer colony size on autumn colony size was evaluated with the same GLMM modeling method (Gaussian distribution, Identity as link function, and apiary as random effect). The effects of colony size and *V. destructor* infestation rates (alone and of their interaction) in autumn on winter mortality were investigated with a Bernoulli model (i.e., a GLMM with a binomial distribution, a logit function as link, and apiary as random effect). We combined these variables in a single model because they act in concert on colony health, but we also modeled them separately to assess their individual effects on the response variable, winter mortality.

The evaluation of the p value (significant p value ≤ 0.05) of the variables in the models was estimated with Satterthwaite approximation (Kuznetsova et al., 2017). Because the area of implementation of agroecological measures changed over years, and because intense variations in yearly climatic conditions are common, GLMMs were applied on the three study years separately, instead of adding the factor "year" as a random effect in a global model. Additionally, the random effect of "year" is partially absorbed by the random effect of "apiary" (Kretzschmar et al., 2016).

RESULTS

Identification of the contribution of agroecological measures to the meadow structures surrounding the apiaries

PCAs showed that the distribution pattern of the meadow types (temporary, permanent, and ecological) was consistent from year to year over the three years. The meadow types showing the most variable surface area within the sectors over the three years were: temporary meadow mowed without conditioner, temporary meadow with unmown floral strips, the combination of the latter two, and temporary meadow mowed without conditioner after flowering, that is, with delayed mowing (see Appendix S1: Figure S1). Because of this consistency, the meadow types used for further analysis were selected based on a new PCA run on the pooled data of the three years (see Appendix S1: Table S1). As observed in the correlation circle in this PCA, temporary meadows mowed without conditioner, as a single measure or in combination with floral strips or with delayed mowing, and temporary meadows with floral strips as a single measure are strongly correlated with dimension 1 (inertia = 28.6%) and contributed to more than 93.6% of the distribution of apiaries on the plane defined by the first two dimensions (Figure 3; Appendix S1: Table S2). Permanent meadows mowed without conditioner and permanent meadows without measures, as well as to a lesser extent, temporary meadows with delayed mowing correlated with dimension 2 (inertia = 22.0%) and contributed to 77.2% of the total inertia (Appendix S1: Table S1). Ecological meadows and temporary meadows without measures correlated with dimension 3 (inertia = 15.4%) with respective contributions of 40.2% and 25.1% (Appendix S1: Table S1). These results suggested focusing the analysis on temporary meadows with and without agroecological measures, on temporary meadows with floral strips, and on temporary meadows mowed without conditioner as a single measure or in combination with floral strips or with delayed mowing.

The surface area of temporary meadows mowed without conditioner increased from 17.6 ha/sector in 2018 to

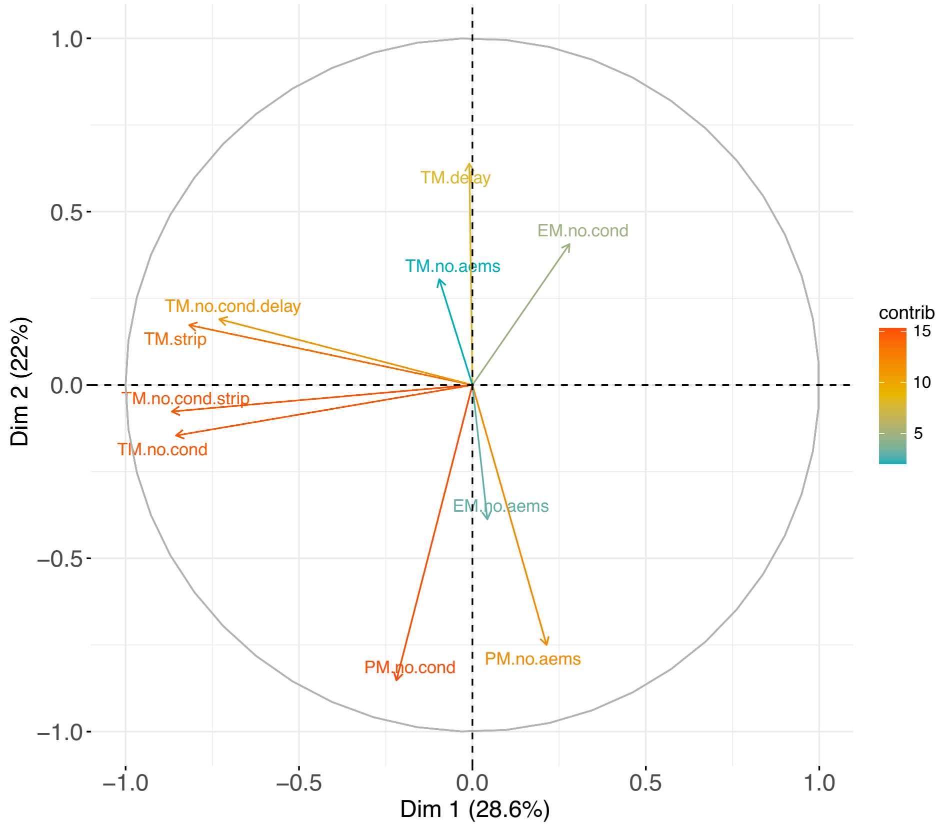

FIGURE 3 Correlation circle of the distribution of meadow types with and without agroecological measures according to dimensions 1 and 2 of the principal components analysis. Percentage of inertia for dimension 1 (Dim 1) and dimension 2 (Dim 2) is given in parentheses. The contributions of the variables are expressed in percentage by a gradient of colors indicated under 'contrib'. TM.no.aems, temporary meadows without agroecological measures; TM.no.cond, temporary meadows mowed without conditioner; TM.strip, temporary meadows with unmown floral strip; TM.delay, temporary meadows with delayed mowing; TM.no.cond.strip, temporary meadows mowed without conditioner and with unmown floral strip; TM.no.cond.delay, temporary meadows with delayed mowing without conditioner; PM.no.aems, permanent meadows without agroecological measures; PM.no.cond, permanent meadows mowed without conditioner; EM.no.aems, ecological meadow without agroecological measure; EM.no.cond, ecological meadow mowed without conditioner.

22.9 ha/sector in 2020, whereas the surface area of temporary meadows without measures slightly decreased in 2020 (Table 2). The same pattern was observed for delayed mowing without conditioner, while the changes in surface areas of floral strips combined with mowing without conditioner were more variable, with no marked tendency (Table 2).

The four measures were applied over the three years with small variations in the surface areas of meadows. Their total contribution to the first dimension of the PCA was almost constant (91.1%, 93.4%, and 92.0% for 2018, 2019, and 2020, respectively) (see Appendix S1: Table S3).

Effect of the agroecological measures in temporary meadows on spring and summer colony size

In 2018, but not in the other years, a significant positive effect of temporary meadows without measures on the number of adult honey bee workers in June was observed ($p = 0.047$ with fixed $R^2 = 0.05$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). Despite the significant p value, the determination coefficient for the fixed effect fixed R^2 was below 0.10, indicating a relatively small effect. Temporary meadows mowed without conditioner also showed a slight positive, albeit nonsignificant, effect on the number of adult honey bee workers in June 2018 ($p = 0.082$ with fixed $R^2 = 0.09$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). In 2019, there was a slight significant positive effect on the number of adult honey bees in June associated with the mowing without conditioner combined with the presence of unmown floral strips ($p = 0.04$ with fixed $R^2 = 0.06$), and a trend for the effect of delayed mowing ($p = 0.06$ with fixed $R^2 = 0.05$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). In June 2020, July 2018, 2019, and 2020, there was no significant effect of any agroecological measure on the number of adult honey bee workers.

TABLE 2 Total surface area (in hectares) of the agroecological measures implemented in temporary meadows in the 30 study sectors over the three-year study.

Temporary meadows with and without agroecological measures	2018	2019	2020
Temporary meadow mowed without conditioner	17.60	19.46	22.91
Temporary meadow with unmown floral strips	1.56	0.94	1.41
Temporary meadow with delayed mowing	5.50	5.28	3.80
Temporary meadow mowed without conditioner and unmown floral strips	2.98	3.39	1.43
Temporary meadow mowed without conditioner and delayed mowing	5.14	5.45	5.40
Temporary meadow without agroecological measures	99.60	106.78	81.61

There was neither a significant effect of the selected agroecological measures on the amount of brood in June and July 2018 nor in June 2019 (all $p > 0.05$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). By contrast, a significant positive effect on brood was observed at the end of July 2019 when mowing without conditioner alone and combined with unmown floral strips or with delayed mowing were applied (p values ranging from 0.02 to 0.002 with fixed R^2 ranging from 0.10 to 0.22; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). In July 2019, the effect of mowing without conditioner was also significant when temporary meadows without measures were added as an additional variable in the model ($p = 0.016$ with fixed $R^2 = 0.14$). The same pattern was observed in July, but not in June, of 2020, with a significant positive effect of temporary meadows mowed without conditioner ($p = 0.022$; fixed $R^2 = 0.08$) and of delayed mowing ($p = 0.035$; fixed $R^2 = 0.07$).

Effect of the spring and summer colony size on the number of adult honey bees and brood in autumn

In June and July for all years, the number of adult honey bees was correlated with the number of capped brood cells (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). For each of the three years, the number of adult workers in July had a significant positive effect on colony size in October ($p < 0.04$ with fixed R^2 between 0.08 and 0.04; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). However, the number of adult workers in June did not significantly correlate with colony size in October (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). The positive effects of the amount of brood in June and in July on colony size in October were occasionally significant only in 2019 and 2020 but never in 2018 (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1).

Effects of colony size in autumn and *V. destructor* on winter mortality

When the number of adult honey bees and capped brood cells was considered in a mortality model, the two variables had divergent effects. The number of adults had a significant positive effect on survival in the three years ($p < 0.005$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). By contrast, the number of capped brood cells had no effect in 2018 and 2020, whereas in 2019, a significant positive effect on survival was observed (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). For each of the three study years, *V. destructor* infestation rates in autumn, when considered as the single variable in a mortality model, were significantly associated with higher winter mortality ($p < 0.009$; fixed $R^2 > 0.03$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). When the number of adult honey bees, capped brood cells, and the *V. destructor* infestation rates were included as variables, only the positive effect of the number of adult honey bees on colony survival in 2019 and 2020 remained significant ($p = 0.028$ and $p = 0.001$, respectively). In 2018, a positive trend was observed for adult honey bees ($p = 0.07$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). There was no significant interaction between *V. destructor* infestation rates and colony size ($p > 0.310$; see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1).

DISCUSSION

The objectives of our study were to evaluate the effects of agroecological measures applied to meadows on honey bee colonies development and survival. For this, we evaluated whether the surface areas of meadows under agroecological management in the flight range of the colonies were associated with increased summer and autumn colony sizes and decreased winter colony mortality. Colony size in July was positively influenced by three agroecological measures on temporary meadows (i.e., mowing without conditioner, leaving floral strips unmown, and delayed mowing combined with mowing without conditioner). In July, the amount of brood and even more so the number of adult honey bees had a positive effect on colony size in autumn. In turn, colony size in autumn, again mainly the number of adult honey bees, was associated with better colony overwintering. We thus gathered evidence that the agroecological measures applied to temporary meadows promote the development of the colonies positively, which increases their probability of survival over winter (Figure 4).

Selected agroecological measures in temporary and permanent meadows around apiaries

Four agroecological measures implemented in temporary meadows contributed most to the first two dimensions of the yearly PCAs (with an average contribution of 92% to dimension 1; Appendix S1: Table S3). Despite changes in surface area (Table 2), the contributions of these four measures were consistent over the three years of observations and targeted temporary meadows. These measures were the mowing without conditioner alone or in combination with delayed mowing or with leaving unmown floral strips, and the floral strips alone. A beneficial effect of temporary meadows without agroecological measures on colony size was observed only in 2018 and not in 2019 and 2020. These results suggest that the resources normally available in meadows were not at the origin of the beneficial effects observed, at least not for 2019 and 2020, and that these effects indeed resulted from the agroecological measures implemented (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1).

The agroecological measures were less frequently employed in permanent meadows (Table 1). Permanent meadows on which no conditioner was used or without any measures were strongly correlated with dimension 2, which means that the areas of the permanent meadows over the 30 sectors around apiaries varied independently from those of the temporary meadows (Appendix S1: Table S1). Additionally, their contributions to land-use structure were lower than that of temporary meadows (Appendix S1: Table S3).

Effects of selected agroecological measures in temporary meadows on colony size

The mowing of temporary meadows without conditioner, the delayed mowing without conditioner, and the presence of floral strips in meadows mowed without conditioner had significant positive effects on brood size in July 2019 and 2020, but not in 2018 (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). This pattern may be related to an insufficient surface area on which these agroecological measures were implemented in the first year and to their annual increase above an

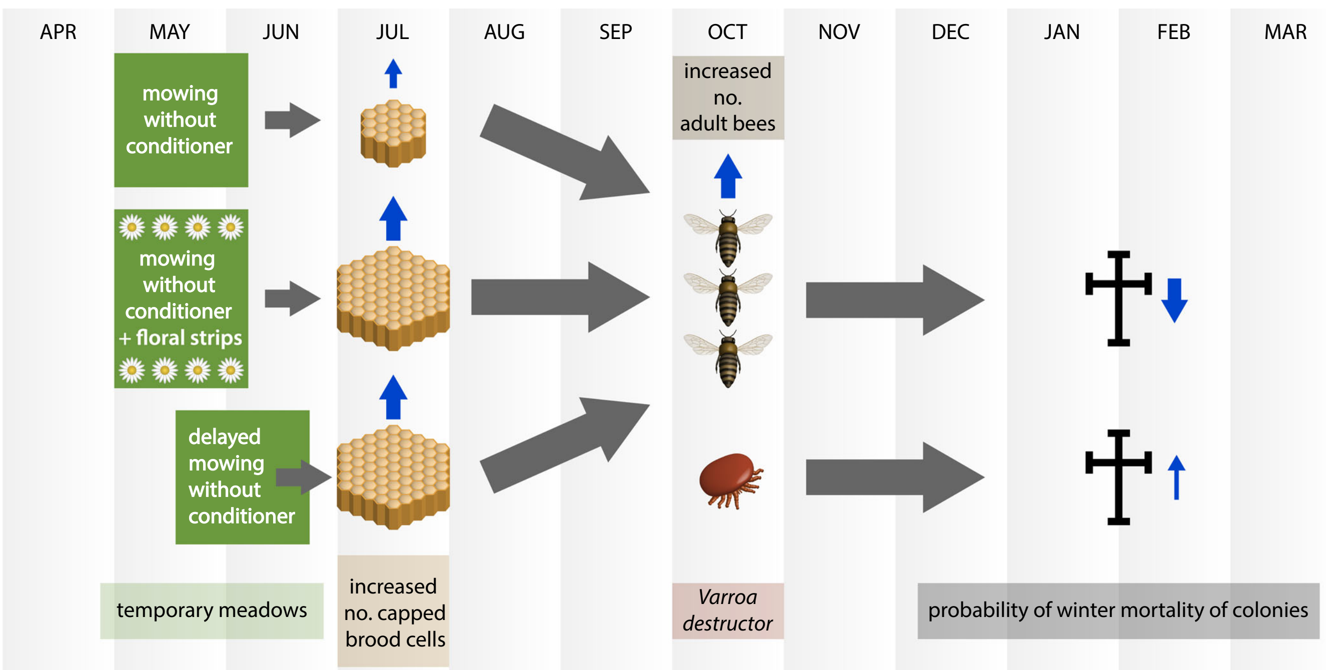

FIGURE 4 Graphical summary of the main cascading beneficial effects on colony development and winter survival of the three agroecological measures on temporary meadows.

effective threshold in the following years (of 5.4% in 2019 and 6.7% in 2020; calculated from data in Table 2). It is therefore possible that if these surface areas further increased, their beneficial effects on honey bee colony size would also rise. Despite low values of the coefficients of correlation R^2, it is possible to approximate the effect of these measures on the number of capped brood cells. The number of capped brood cells could increase from a thousand to almost three thousand for every 10-ha increase in surface area on which the various measures were implemented. Another explanation for the fact that we did not detect an effect in 2018 could be due to suboptimal beekeeping practices, in particular regarding the treatments against *V. destructor* (Correia, 2021; Hernandez et al., 2022). The negative effects of excessive *V. destructor* infestation rates on brood production (Hernandez et al., 2022) could have masked the effects of the agroecological measures.

We could find no significant effect of foregoing the use of a conditioner while mowing on the number of adult workers in June or July, despite the fact that forager bees are directly exposed to the conditioner, whereas brood cells are not at all exposed to it. Mowing without conditioner thus likely affected the amount of brood indirectly. Foregoing the use of this device could have resulted in higher numbers of foragers returning to the colony with resources, which benefited brood rearing by the colonies. This measure might alleviate the need for colonies to compensate for foragers killed by conditioner (Fluri & Frick, 2002), thus allowing the honey bee nurses to continue caring for the brood instead of exiting the hive to forage. Indeed, a lack of foragers promotes the behavioral maturation of nurses, which start foraging to maintain colony resources (Eyer et al., 2017; Johnson, 2010; Sagili et al., 2011).

A positive effect on the number of adult bees in June 2019 and on the amount of brood in July 2019 and 2020 was detected when the mowing of temporary meadows without conditioner was combined with the presence of unmown floral strips or with delayed mowing. This effect was most certainly due to the floral resources that these agroecological measures provided, increasing the availability of pollen and nectar for the colonies. These results suggest that the effect of mowing without conditioner was enhanced when combined with the floral strips or with delayed mowing. Delayed mowing appeared as effective as floral strips at promoting honey bee colony size (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1).

As a result of the high correlation between the number of brood cells and adult honey bees, we can consider that, despite some nonsignificant relationships in our models (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1), the positive effect of agroecological measures observed on capped brood cells in July implied the same effect on adult honey bee numbers. Consequently, we can assume that agroecological measures also had a positive effect on colony size in July.

Colony size in the spring is influenced by several interrelated factors (i.e., climate, genetics), and therefore differences in colony dynamics may mask the positive effect of the agroecological measures that could act as levers reinforcing colony development in the spring and summer. Despite the high number of uncontrolled factors in our field study involving volunteers (e.g., unforeseeable but necessary beekeeping actions at the end of summer, such as feeding, colonies merging, or queen replacement), which could influence colony development, we observed a positive effect of the colony size in July on the colony size in October, before wintering (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). This relationship was slightly decreased by high *V. destructor* infestation rates, which were possibly due to suboptimal treatments between late summer and autumn (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). This result indicates that effective *V. destructor* treatments are crucial to ensure honey bee colony health and to allow colonies to benefit from agroecological measures implemented in agricultural landscapes.

Colony size and winter survival

The size of a colony in autumn had an important influence on its overwintering survival probability (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). The number of adult honey bees in autumn had a significant negative effect on the mortality probability, that is, a high number of adult bees in October led to low winter mortality. We observed that when *V. destructor* infestation rates in October, which are known to be an important determinant of colony survival over winter (Giacobino et al., 2015; Hernandez et al., 2022), are added to the model, the effect of the number of adult honey bees remained significant (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). The number of adult honey bees in autumn thus appears to be as important as the *V. destructor* infestation rates before winter in determining colony survival over the cold season (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). It is thus likely that agroecological measures, which lead to an increase in the number of honey bees during the flowering season would subsequently increase colony resilience to infestations by this parasite in autumn. However, this effect is unlikely to be sufficient to counter high infestation rates due to suboptimal varroacidal treatments, for example (Hernandez et al., 2022).

The effect of the number of capped brood cells on colony survival was more variable. This effect was only significantly positive in 2019 (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1) and became nonsignificant when the variable *V. destructor* infestation rates in October was added to the model (see associated dataset: https://doi.org/10.5061/dryad.pg4f4qrt1). This variability may be due to beekeepers replacing queens or to natural queen replacements in September. The associated interruption of brood production would thus bias the measurement of colony size in October. This variability may also be due to yearly climatically induced variations in the timing of brood production decline toward the end of summer (Kretzschmar & Frontero, 2017; Odoux et al., 2014).

Robustness of the effects of agroecological measures to climatic variations

It is important to consider that the observations were made over three years (2018, 2019, and 2020) with different climatic conditions and, consequently, different colony development patterns. Annual climatic variations affect the availability of floral resources (pollen and nectar) and hence the amount of brood that can be reared by the colonies and in turn the number of emerging adult workers (Kretzschmar & Frontero, 2017; Odoux et al., 2014). The cascade of beneficial effects of the agroecological measures on colony size in summer and autumn and on winter mortality was, however, consistent across the three years. Our findings thus suggest that these agroecological measures may be robust against climatic variations in the range of those experienced during the three study years.

CONCLUSION

Our data indicate that colony size in July, that is, the number of adults and capped brood cells, was enhanced by the agroecological measures implemented in temporary meadows, that is, mowing without conditioner, floral strips, and delayed mowing. A high number of adult and immature honey bees in July led to a large colony size in autumn. In turn, the high number of workers populating colonies ahead of winter increased colony survival over the cold season. The number of workers at this time of the year was, however, negatively affected by high *V. destructor* infestation rates, which can be prevented by well-implemented varroacidal treatments (Hernandez et al., 2022).

Although implemented on relatively small surface areas (approximately 4% of the sectors of 2-km radius around apiaries), we found evidence that agroecological measures in temporary meadows had significant effects on the improvement of the honey bee colonies development and survival. The detection of a link—although slight—between agroecological measures and colony strength is noteworthy given the variety of factors interacting with colonies development and health (beekeeping management, climatic conditions, pathogens, etc.). Further evaluation of the effects of agroecological measures on honey bees could be complemented by an evaluation of their cost-efficiency and by extending such monitoring efforts to designs with more controlled conditions and to other types of meadows (permanent and ecological).

Our results advocate for an expansion of measures on temporary meadows, and especially of their combination, which enhanced the effect of single measures. They also show that both beekeepers and farmers can contribute to increased honey bee colony health and suggest that concerted actions promoting the well-being of these pollinators can benefit both parties.

AUTHOR CONTRIBUTIONS

Conceptualization: Julie Hernandez, Yann-David Varennes, Alexandre Aebi, Vincent Dietemann, and André Kretzschmar. *Data curation*: Julie Hernandez and Yann-David Varennes. *Formal analysis*: Julie Hernandez and André Kretzschmar. *Methodology*: André Kretzschmar, Julie Hernandez, and Yann-David Varennes. *Supervision*: Alexandre Aebi, Vincent Dietemann, and André Kretzschmar. *Writing—original draft preparation*: Julie Hernandez, Yann-David Varennes, and André Kretzschmar. *Writing—review and editing*: Alexandre Aebi and Vincent Dietemann.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Hernandez, 2022) are available from Dryad: https://doi.org/10.5061/dryad.pg4f4qrt1.

ORCID

Julie Hernandez https://orcid.org/0000-0001-8480-6180
Vincent Dietemann https://orcid.org/0000-0002-0791-9939

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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