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Assessing the diversity of trade-offs between life functions in early lactation dairy cows

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ABSTRACT

This study objective was to develop a method to characterize the diversity of trade-offs between life functions expressed by dairy cows. Trade-offs between life functions involve adaptive responses of dairy cows to suboptimal nutritional environments. Until now, they have been explored mainly by examining unfavorable correlations between two traits. These two-trait approaches are limiting for exploring the diversity of trade-offs among cows. A multi-trait and dynamic method was developed to phenotype trade-offs between life functions involved in cow fitness (lactation, reproduction, and ability to survive) and explore their diversity. Records from 334 lactating cows reared in two experimental INRA (France) units were used to study the dynamics of cow milk yield, body condition changes and reproduction performance. The analysis focused on the first 13 weeks postpartum, when cows are supposed to experience a negative energy balance. Ten variables accounting for the dynamics of responses were calculated and included in a clustering analysis. Four main clusters of trade-offs were obtained. Profile 1 of trade-off ($N=53$) included cows giving priority to lactation and mobilizing much of their body fat reserves, with poor reproductive performance. Trade-off profile 2 ($N=111$) identified cows mobilizing much of their body fat reserves, giving priority to reproduction at the expense of high milk yield. Trade-off profile 3 ($N=67$) consisted of thin cows presenting difficulties in all functions: a large body-reserve mobilization after calving that does not benefit to milk yield and long delays before reproducing and low success rates. Profile 4 of trade-off ($N=103$) was composed of cows with no trade-off between functions, since they recorded average milk yield, maintained their body condition and had good reproductive performances. Our approach highlighted the relevance of considering the three life functions simultaneously when phenotyping dairy cows for their ability to manage prioritization between life functions and this multi-trait clustering approach represents an operational tool to do so, using readily available farm data. Since classification of cows into clusters is not fully determined by the breed or parity, our study underlined also the utility of better understanding the mechanisms that drive nutrient allocation between life functions. We also believe in the benefit of considering this individual diversity, as a herd management tool for farmers.

1. Introduction

In ecology, trade-offs represent unfavorable associations that exist between life history functions (Zera and Harshman, 2001). Trade-offs result from the expression of genetically driven mechanisms (Roff et al., 2002) that ensure the fitness of animals when resources are limited (Blanc et al., 2006). They result from priority rules for nutrient allocation implemented in limited environments, i.e. in situations in which the pool of available nutrients (intake and body mobilization) do not meet the energy demand for life functions (Glazier, 2009). In animal science, the term "trade-offs" is generally used to describe the expression of

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unfavorable genetic correlations (Windig et al., 2006) observed between production traits accounting for physiological functions (e.g. growth, lactation, and reproduction) in constraining environments. In most literature on dairy cows, trade-offs were mainly explored by studying the expression of unfavorable genetic associations between only two traits (Hoekstra et al., 1994, Pryce et al., 1997). However, several studies reported that high-yielding dairy cows exhibit trade-offs between several functions: milk production, growth and reproduction during energy-restricted situations, such as during early lactation (Friggens et al., 2010). When animals selected for milk production have a negative energy balance (**NEB**) (Gross et al., 2011), nutrient partitioning is genetically driven toward lactation to the detriment of other functions such as reproduction (Friggens and Newbold, 2007, Friggens et al., 2013).

We considered that the main functions of interest in dairy cows are lactation, reproduction, and the ability to cope with external stressors and survive. The first two functions can be studied through milk production records and reproductive traits (time of conception, pregnancy success rate, etc.). The last function is most difficult to ascertain with direct traits or indicators because the cow lifespan strongly depends on the culling rules defined by the farmer. Furthermore, giving such an assessment would imply having indications on health, well-being status and metabolic capacities to cope with stressors. Body condition score (**BCS**) is an assessment of animal fat reserves and provides an estimate of body-reserve mobilization when a cow is in NEB (Roche et al., 2009). BCS changes give information about the flexibility provided by body fat reserves to adapt to and buffer against nutritional changes (Gearhart et al., 1990, Friggens, 2003). BCS can also be an indirect indicator of animal health when frequently assessed (Berry et al., 2008) and provides relative information about cow welfare (Roche et al., 2009). In addition, BCS is easily measurable on farm at low cost. Therefore, BCS could be considered an acceptable indicator to evaluate the ability of dairy cows to cope with external stressors and survive in restricted nutritional environments.

Several studies approached trade-offs in dairy cows through experiments that included nutritional challenges and separately compared milk yield, BCS and reproduction responses (Dillon et al., 2003, Horn et al., 2014). In these previously mentioned studies, performances and trade-offs expressed by dairy cows were analyzed separately by breed and parity, assuming that breed and parity are significant drivers of trade-offs. To move beyond this hypothesis, we investigated trade-offs independently from individual cow characteristics and used them a posteriori as potential explicative factors for the diversity of trade-offs expressed by dairy cows.

As suggested by Friggens and Newbold (2007) and Friggens and Van der Waaij (2009), we make the hypothesis that trade-offs between physiological functions should be studied through a multi-trait approach. We also hypothesize that trade-offs should be studied with dynamic rather than static approaches to investigate biological response changes over time (Roff et al., 2002) and use short-time-step analysis (Friggens and Van der Waaij, 2009). This study objective is to characterize trade-offs diversity in dairy cows by using a multi-trait clustering approach jointly analyzing the dynamics of the three main life functions: lactation, reproduction and the ability to adapt and survive.

2. Material and methods

2.1. Data

This study is based on analyzing data from dairy cows enrolled in three long-term experiments conducted at two INRA (France) experimental units. Cows at both sites were housed during winter and grazed for the rest of the year. The first experiment was conducted on the Mirecourt farm (48.3°N, 6.13°E) in northeastern France from 2000 to 2003 with Holstein and Montbéliarde cows reared as one herd in a conventional system and fed forage (maize and grass silage) ad libitum and 4 kg/cow/d of concentrates (barley and protein meal). Cows in this system were part of the Mirecourt High Energy Diet group (**M-HED**). The second experiment was conducted from 2004 to 2012 at the Mirecourt experimental dairy farm, also with Holstein and Montbéliarde cows. Two organic systems were designed for the experiment: a Grass-based System (**M-GS**) and a Mixed-crop dairy System (**M-MS**), as described by Gouttenoire et al. (2010) and Coquil et al. (2014). Cows from the M-GS were fed only forage (grass and hay) with maximum grazing achieved by grouping the calving season over a three-month period in late winter. Cows enrolled in the M-MS calved over a three-month period in autumn and were fed 2–4 kg of concentrates (barley or oats and peas or lupine) and forage (90% hay and 10% silage or haylage). The third experiment was conducted on the Le Pin-au-Haras (48.4°N, 0.09°E) experimental dairy farm in northwestern France from 2006 to 2011 with both Normande and Holstein cows. In this experiment, cows were equally distributed in two herds that were fed two different diets, as described by Cutullic et al. (2011). The first diet, characterized by a Low Energy Diet (**L-LED**), was based only on forage with a winter total mixed ration of 50% grass silage and 50% haylage and a spring-to-autumn ration exclusively based on grazing. The L-LED reproduction period was restricted from April to June to synchronize the cows' energy requirements with grass growth. The second group, characterized by a High Energy Diet (**L-HED**), received a total mixed ration in winter composed of 55% maize silage, 15% dehydrated alfalfa and 30% concentrates, and a spring to autumn diet based on grazing supplemented with 4 kg of concentrates/cow/d and 5–8 kg of maize silage/cow/d if a significant drop in grass growth was observed. Cow drying-off and reproductive management followed common rules in both experimental units to keep calvings grouped within a 91 d target period. Cows were dried-off 60 d before presume calving date and fed grass silage. Cows with BCS $>$ 2, three months before calving were dried-off earlier. Calendar-based starting and ending dates for the breeding season were defined each year within each experiment to keep calvings grouped within a 91 d target period. The starting date was either the herd starting date of the breeding season for cows calved at least 42 d before this calendar date or the calving date of the cow plus 42 d for cows calving after the herd calendar starting date. Thus, all animals were given at least 42 d between calving and first service, but the length of the breeding season differed for each cow according to its previous calving date. Cows were inseminated at natural estruses when observed from their starting date to the ending date of the breeding season. Consequently, the length of the breeding season differed for each cow, with a maximum of 13 weeks. In all experiments, each cow was monitored for milk production, body condition, and reproductive and health events. The dataset for each cow included: weekly milk records; BCS, scale 0 = thin to 5 = fat (Agabriel et al., 1986); breeding events: calving date, service dates, conception date; and individual information: date of birth, lactation rank, breed, and age at calving. BCS was recorded at calving and at least every month postpartum. Lactations with abnormal milk-yield values, i.e. when a recorded milk yield was less than 50% of the previously recorded milk yield (Wiggans et al., 2003), were fully excluded from the dataset. Similarly, extended lactations of more than 525 d, as defined by Grossman and Koops (2003), were removed from the dataset. Cows included in the dataset produced an average of 6035 ± 1695 kg of milk per lactation (Table 1). The average

Table 1
Performance and characteristics of dairy cows included in the dataset according to their enrollment in the different experimental systems.

Item[a]	Experimental system[b]									
	L-LED		L-HED		M-HED		M-GS		M-MS	
Cow number	32	SD	68	SD	123	SD	73	SD	38	SD
Lactation yield (kg)	5476	943.7	7902	1927.7	5783	1282.5	4853	925.5	6249	1269.9
Milk at peak (kg/d)	26	4.8	36	8.6	30	5.3	27	5.3	29	5.4
Lactation length (d)	319	40.0	327	39.7	301	43.8	287	37.3	365	56.7
BCS at calving	3.2	0.64	3.5	0.62	2.9	0.59	2.5	0.56	2.2	0.56
BCS average	2.3	0.51	3.0	0.67	2.4	0.56	1.9	0.28	1.9	0.38
IBC (d)	35	29.9	35	23.2	43	38.5	28	28.7	79	38.4
IBCalving[4] (d)	410	132.0	403	132.4	389	109.1	439	137.5	508	102.3
NS	1.5	0.88	1.8	1.14	2.3	1.52	2.0	1.18	2.6	1.62
Age at 1st calving (y)	3.0	0.00	2.8	0.38	2.1	0.39	2.4	0.49	2.2	0.47
Parity	2.0	1.18	2.0	1.27	2.4	1.50	2.3	1.23	2.6	1.75

[a] BCS=body condition score (from 0 to 5), IBC=Interval between the start of the breeding season and the date of conception (excluding saturated values attributed to non-pregnant animals), IBCalving=Interval between the starting day of the breeding season and the following calving, NS=number of services.
[b] L-LED=Low energy diet system of Le Pin-au-Haras, L-HED=High energy diet system of Le Pin-au-Haras, M-HE=High energy diet system of Mirecourt, M-GS=Organic grass-based system of Mirecourt, M-MS=Organic mixed-crop dairy system of Mirecourt.

lactation length was 312 ± 47 d. There were 126 primiparous lactations and 208 multiparous lactations ranging in parity from 2 to 9. Three cow breeds were represented in the database: Holstein (N=162), Montbéliarde (N=115) and Normande (N=57). Most cows (N=244; 73%) recalved, whereas 90 failed to reproduce. Overall, the database contained records for 334 lactations, with 234 from Mirecourt cows and 100 from Le Pin-au-Haras cows (Table 1).

2.2. A study period to observe trade-offs

A common period of expected NEB was identified for all individuals in the different experimental herds to characterize trade-offs between life functions. Butler (2003) reported that dairy cows are in NEB during early lactation and demonstrated that NEB could last up to 12 weeks after calving. Therefore, the 334 lactations were studied only during the period from calving to 13 weeks postpartum.

2.3. A set of variables to characterize trade-offs dynamics

Trade-offs for each individual were characterized among the three main functions of interest: lactation, reproduction and body fat reserves usage. Each life function can be characterized through several traits. A multi-trait approach was developed to account for temporal changes in the prioritization of nutrients among the three life functions. The selected traits were representative of the phenotypic response dynamics. Each trait was then broken down into several variables. The functional and production traits were studied using variables representative of temporal changes in milk production and BCS and considered delay in and success of reproduction. Variables were defined in two steps. First, a set of variables for each trait was calculated to represent their dynamics (i.e. slope direction and magnitude of variation) during the period (Appendix A1). Second, we selected a subset of variables for each set based on analysis of inter-correlations using Pearson coefficients (r) and biological plausibility (Appendix A2). Details for each life function are as follows:

2.3.1. Milk production

Weekly average milk records were analyzed to follow individual temporal changes in milk production during the first 13 weeks postpartum. From these raw data, we calculated a set of variables (Appendix A1) to quantify the amount of milk produced and describe the shape of the lactation curve over the first 13 weeks of lactation. Then, the three least correlated variables ($|r| < 0.7$) from this set were selected: the Average Milk Yield over the period (**AMY**), calculated as the average of weekly milk yields; the daily average Milk Yield at the 13th Week of lactation (**MYW_{13}**) and the interval (d) between Calving and the postpartum week with the highest milk yield recorded during the study period, which we called the Milk Peak (**CMP**).

2.3.2. Body condition score

BCS was recorded at calving and then measured monthly. Thus, each cow had its BCS recorded 4 times during the study period. Similar to milk production, we calculated a set of variables (Appendix A1) to describe the direction and magnitude of BCS changes over the period. We kept the four least correlated variables ($|r| < 0.7$): BCS at calving (**BCSc**); the number of times that BCS decreased from month-to-month (**N_ΔBCS < 0**), calculated as the number of month when $BCS_n - BCS_{n-1} < 0$; the number of times that BCS did not change from month-to-month (**N_ΔBCS=0**), calculated as the number of weeks where $BCS_n - BCS_{n-1} = 0$; and the relative change (**ΔBCS**, %) in BCS between calving (BCSc) and week 13 postpartum (BCS_{W13}), calculated as $(BCS_{W13} - BCSc)/BCSc \times 100$.

2.3.3. Reproduction

Three variables were calculated for each individual and kept for analysis based on their low interdependence ($|r| < 0.4$). The first variable was the number of days between the starting date of the breeding season defined for each cow according to the rules previously described and their first service (**IBS1**). The second variable was the number of days between the starting date of a cow's breeding season and its date of conception (**IBC**). For the cows that failed to conceive, a maximum value of saturation (220 d) was defined as the maximum value of IBC recorded in our dataset plus one standard deviation. The last variable was the number of services per cow during the breeding season (**NS**).

2.4. Statistical methods to discriminate trade-off profiles

Multivariate statistical analysis aimed to discriminate cows according to the 10 previously defined variables describing the combined dynamics of milk production, BCS and reproduction. Data were analyzed using SPAD 7.4 software (Coheris, Suresnes, France). The statistical analysis was conducted in two steps, starting with a principal component analysis (**PCA**), followed by a hierarchical cluster analysis (**CA**). The Kaiser criterion with an eigenvalue greater than 1 was used to determine the number of final principal components. The first four principal components (**PC**) were retained and accounted for 70% of the variability. The CA was used to identify the main clusters of trade-off profiles. The CA used the nearest centroid sorting method (Anderberg, 1973), which iteratively creates clusters by minimizing the distance between individuals and the cluster average calculated from the values of the 4 PCs. This multivariate analysis was conducted a priori, without considering explanatory variables, to focus only on nutrient-allocation prioritization and preclude any preconceptions about potential effects of breed or parity, etc. The resulting clusters were then characterized by their main descriptive variables (parity, breed, age at first calving, reproduction success and total lactation milk yield). Differences between clusters were assessed for each descriptive variable with a Tukey's test for numbers comparison or a Chi-square test for proportions comparison. These tests were performed using RStudio (version 0.98.978) software (Boston, USA).

3. Results

3.1. Four main clusters associated to four contrasted trade-off profiles

The first PC represented 25.7% of the total variation and discriminated individuals mainly on the basis of their BCS dynamics, with either negative or stable BCS over the study period. The second PC accounted for 17.2% of the total variance and opposed individuals with high AMY to those whose BCS decreased. The third PC (15.4% of the remaining variation) separated individuals with high BCSc and high AMY from those with long IBS1 intervals and high NS. The fourth PC (12.1% of the remaining variation) distinguished individuals with high NS from those with long CMP and IBS1 intervals. The CA identified the following four main clusters of individuals (Table 2 and Fig. 1).

3.1.1. Trade-off profile 1: high milk yield at the expense of BCS maintaining

The first cluster (trade-off profile 1) contained 53 lactations (16% of the dataset). Cows in this group had higher AMY (487 kg, $p<0.001$) and marginally longer CMP intervals (49, $p=0.117$) than the other profiles (Table 2). They mobilize a large part of their body reserves with a decrease of 32% of their BCSc over the studied period (Fig. 2). They were generally inseminated later after the start of the breeding season (IBS1 = 20 vs. $p<0.05$) than the profiles 3 and 4. Their pregnancy rate of 64% was significantly lower than the pregnancy rate of profile 4 but significantly higher than in profile 3 ($p<0.001$, Table 2).

3.1.2. Trade-off profile 2: good reproduction success rate at the expense of BCS maintaining and high milk yield

The second cluster (trade-off profile 2) included 111 lactations (33% of the dataset). The average AMY of profile 2 was the lowest among all profiles with 320 kg of milk produced over the studied period, even if it did not significantly differ from the AMY of profiles 3 and 4 (Table 2). These cows experienced the greatest decrease in BCS during the 13-weeks postpartum period, with a loss of 35% of their BCSc. Nevertheless their ΔBCS was not significantly different from the one of profile 1. Cows from profile 2 ensured their reproductive function (71% of reproduction success), with an intermediate IBC interval of 72 d regarding the other profiles (Fig. 2).

3.1.3. Trade-off profile 3: low BCS with average milk yield and low reproduction success

The third cluster (trade-off profile 3) included 67 individual lactations (20%) that produced 331 kg over the period which was significantly lower than profile 1 but did not significantly differed from profile 2 and 4. Cows in this profile were mainly characterized by low BCSc (2.5 ± 0.70) and a 23% decrease in BCS from their initial condition during the first 13 weeks of lactation. Compared to the other profiles, these animals combined a low body condition and a non-negligible body reserves mobilization, resulting in very thin animals (BCS < 2) at the beginning of the breeding period (Fig. 2). The pregnancy rate was significantly lower in this profile (30 %, $p<0.001$) compared to the other profiles. Low reproduction success in this cluster was associated with a longer IBC, IBC_P (considering only pregnant cows) and NS than in the other clusters (189 d, 89 d and 3.8 d respectively, $p<0.001$). This profile corresponds to animals with a lower BCSc than those of the two previous profiles (2.5 vs. 3.2 for profile 1 and 3.1 for profile 2); so with potentially less body reserves after parturition to supply energy for metabolic functions.

Table 2
Variables characterizing the four trade-off profiles resulting from the principal component analysis (PCA), their average and their standard deviation (SD).

Item[1]	Trade-off profiles								All		*p*-Value[2]
	Profile 1		Profile 2		Profile 3		Profile 4				
Cow number	53	SD	111	SD	67	SD	103	SD	334	SD	
AMY	487^a	69.1	320^b	59.0	331^b	58.4	331^b	71.0	353	87.0	0.001***
MYW_{13}	35^a	4.1	22^b	3.8	23^b	4.1	23^b	4.5	25	6.0	0.001***
CMP	49	19.9	42	26.0	39	21.7	39	22.9	42	23.4	0.117NS
BCSc[4]	3.2^a	0.63	3.1^a	0.60	2.5^b	0.70	2.8^b	0.78	2.9	0.73	0.001***
N_ΔBCS < 0	2.09^a	0.68	2.36^a	0.53	1.55^b	0.66	0.77^c	0.44	1.66	0.87	0.001***
N_ΔBCS = 0	0.62^a	0.74	0.38^a	0.50	1.00^b	0.83	1.71^c	0.89	0.95	0.93	0.001***
ΔBCS (%)	32^a	16.6	35^a	15.2	23^b	15.0	8^c	14.8	24	19.0	0.001***
IBS1	20^a	13.6	20^a	18.0	14^b	12.9	14^b	13.3	17	15.1	0.042*
IBC	99^a	90.6	72^a	79.6	189^b	52.1	39^c	41.3	89	85.6	0.001***
IBC_P	33^a	24.0	34^a	26.4	89^b	17.0	33^a	26.5	36	24.5	0.001***
NS	1.9^a	1.14	1.5^a	0.78	3.8^b	1.51	1.8^a	0.95	2.1	1.36	0.001***
Pregnancy rate (%)	64^a		71^a		30^b		92^c		68		0.001***

[a–d] Means with superscripts differ significantly by row.

[1] AMY = Average weekly milk yield over the study period (kg); MYW13 = milk yield in the 13th week postpartum (kg); CMP = Interval between calving and the highest average weekly milk yield (d); BCSc = body condition score at calving (0–5); N_ΔBCS < 0 = number of weeks when BCSn − BCSn-1 < 0; N_ΔBCS = 0 = number of weeks when BCSn − BCSn-1 = 0; ΔBCS = BCSweek13 − BCSc/BCSc (%), IBS1 = number of days between cows' starting day of breeding season and first service; IBC = interval between the cows' starting day of the breeding season and conception (d), IBC_P = IBC of pregnant cows only (excluding saturation values), NS = number of services.

[2] *p*-value resulting from Tukey's test (or from Chi-square test for pregnancy rate), assessing the significance of differences between profiles for each variable. NS ($p<0.1$), *($p<0.05$); and ***($p \le 0.001$).

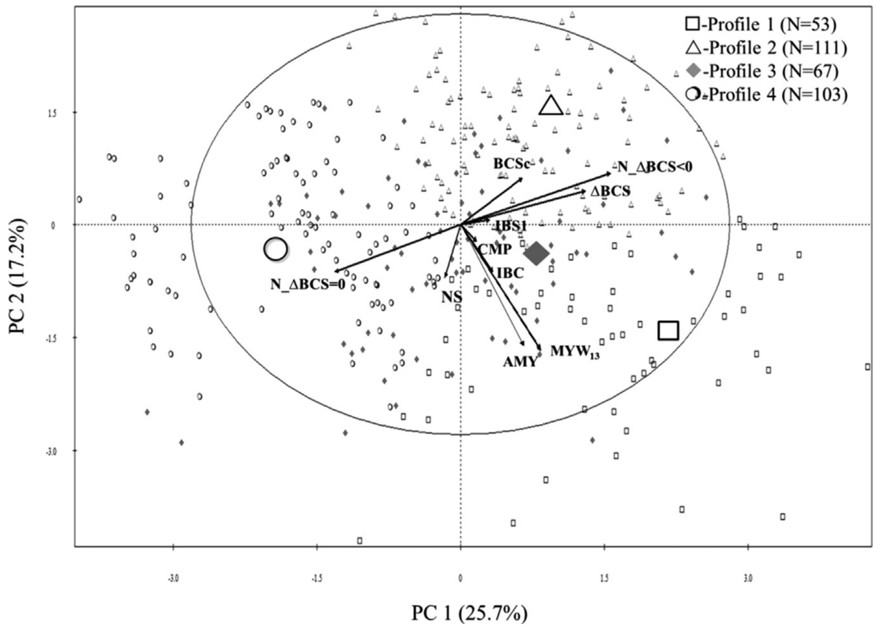

Fig. 1. Plot of the spatial distribution of individuals among the first two principal components (PC) (percentages of the explained variation between brackets) with the correlation circle of variables included in the principal component analysis. MYW_{13}=milk yield in the 13th week postpartum (kg), AMY=sum of the weekly milk yield averages over the study period (kg), IBC=interval between cows' starting day of the breeding season and conception (d), CMP=interval between calving and the highest milk peak (d), BCSc=body condition score at calving (0–5), $\Delta BCS = BCS_{week13} - BCSc/BCSc$ (%), N_ΔBCS < 0=the number of weeks when $BCS_n - BCS_{n-1} < 0$, N_ΔBCS=0=number of weeks when $BCS_n - BCS_{n-1} = 0$, IBS1=number of days between the start date of a cow's breeding season and its first service, NBS=number of services. Centroids of each profile are represented with larger symbols.

3.1.4. Trade-off profile 4: high reproduction success rate, average milk yield and BCS maintaining

The fourth trade-off cluster (trade-off profile 4) included 103 lactations (31%). Cows from this cluster had the highest rate of reproduction success, with only 8% of non-pregnant cows and a short IBC of 39 d. These cows had a low BCSc (2.8) but a relatively stable BCS over the period (ΔBCS=8%). Milk production in this cluster was similar to profiles 2 and 3 and significantly lower than profile 1 (Fig. 2). These results confirm that qualifying cows through their trade-offs profiles is more relevant than discriminating them only on milk production.

3.2. Distribution of breed, age, age at first calving and experimental treatment between profiles

Holstein cows were nearly equally distributed among clusters with 25% of Holstein in profile 1, 30% in profile 2, 22% in profile 3 and 23% in profile 4 (Table 3). Montbéliarde cows were less observed in profile 1 (3% of the Montbéliarde cows), but were well distributed among other profiles (37% in profile 2, 23% in profile 3 and 38% in profile 4). Normande cows were also observed in all trade-off profiles (16% in profile 1, 37% in profile 2, 9% in profile 3 and 39% in profile 4). Cows from different parities were well distributed among profiles (Table 4). Multiparous cows were divided as follow 19% in profile 1, 24% in profile 2, 24% in profile 3 and 33% in profile 4 and primiparous were mainly in profile 2 (48% compared to 10% in profile 1, 14% in profile 3 and 27% in profile 4). Cows allocated to the high-energy diet were well distributed among trade-off profiles with 21% of them in profile 1, 25% in profile 2, 19% in profile 3 and 35% in profile 4. Cows allocated to the low energy diet were found in a higher proportion in profile 2 (50% of them) than in profile 1 (6%), and in profiles 3 and 4 (22% for both). Cows who first calved at two years of age were poorly observed in profile 1 (8% of them) and better represented in profiles 2, 3 and 4 (29%, 27% and 35% respectively, Table 5). Cows who first calved at three years of age were underrepresented in profile 3 (11% of them), overrepresented in profile 2 (39%) and equally distributed between profiles 1 and 4 (26% and 25% respectively).

Looking more in details at each profile composition, it is noteworthy that profile 1 was mostly composed by multiparous Holstein cows fed high energy diet (45% of profile cows) and primiparous Holstein cows fed high energy diet (23% of profile 1 cows). Multiparous Normande cows fed high energy diet were also well represented in this profile (15% of profile 1 cows). It is also remarkable that primiparous cows fed low energy diet were not represented in this profile, independently from the breed as well as cows calving at two years old (30% of cows from profile 1). The profile 2 included cows from all breeds and all parities fed either high or low energy diet. The only significant characteristic was the absence of multiparous Normande cows fed high energy diet. Similarly profile 3 was composed of cows from all breeds and fed both types of diets, but primiparous cows were underrepresented, except for primiparous Holstein cows fed high energy diet (13% of cows from profile 3). Cows from profile 3 mostly calved at two years of age (76% of profile 3 cows). Cows from profile 4 were from all breed and both parities, but cows fed low energy diet (22% of profile 4 cows) were underrepresented compared to cows fed high energy diet (78% of profile 4 cows) and a large part of cows from this profile calved at 2 years of age (65%).

4. Discussion

4.1. Physiology of trade-off in the different profiles

Cows from profiles 1 and 2 that had the highest BCSc experienced the greatest reduction in BCS over the period. This clearly agrees with the results of Garnsworthy and Jones (1987), highlighting the positive association between high BCSc and the extent and duration of body fat mobilization in early lactation. This association is generally accentuated in dairy cows with high genetic merit for milk production (Roche et al., 2009), and correlation analysis of each profile between genetic merit for milk yield and

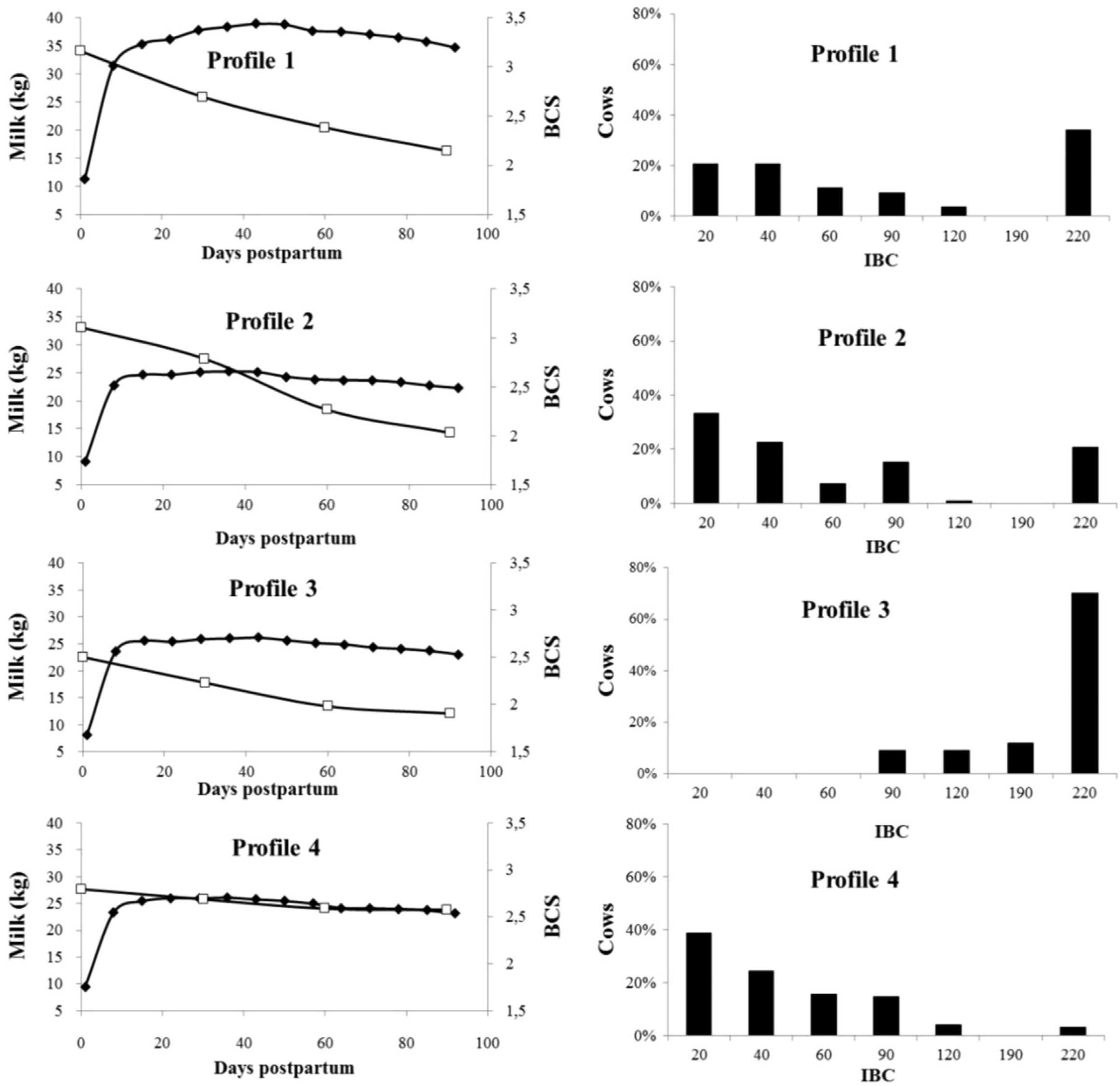

Fig. 2. For each trade-off profile, plots of average milk yield (◆) and body condition score (BCS) (□) evolution over the study period (0–13 weeks postpartum) and plots of cow numbers (in %) according to IBC (interval between the start date of a cow's breeding season and its conception date).

decrease in BCS could provide more insights. The BCS dynamics of cows from profile 3 suggest that these animals had less ability to reconstitute body fat reserves during the previous productive cycle. The low calving rate in this group can be associated with several phenomena. Regarding the low BSCc, followed by a large decrease in BCS indicating severe NEB, we expect that many animals never resumed cyclicity. Similarly, Butler (2003) reported frequent anestrus periods associated with low blood glucose and hormonal abnormalities in early lactation. However, only 9% of cows from this profile were never inseminated. Thus, the reproductive problems of cows from profile 3 were apparently not mainly associated with resumption of cyclicity issues or estrus detection, since the group's IBS1 was the shortest (14 d). Smith and Wallace (1997) observed similarities in multiparous Holstein-Friesian dairy cows, with good resumption of cyclicity (before 21 d postpartum) associated with a longer calving-to-conception interval, a large number of services and low reproduction success rates. In their study, early postpartum luteal activity had no

Table 3
Number of dairy cows in the four trade-off profiles according to their breed (H=Holstein, M=Montbéliarde, and N=Normande) and to their location in the two experimental units.

Trade-off profile	Location 1: Le Pin-au-Haras				Location 2: Mirecourt				Both locations			
	H	N	Both	*p*-Value[1]	H	M	Both	*p*-Value	H	N	M	*p*-Value[1]
Profile 1	27	9	36		14	3	17		41	9	3	
Profile 2	12	21	33		36	42	78		48	21	42	
Profile 3	2	5	7		34	26	60		36	5	26	
Profile 4	2	22	24		35	44	79		37	22	44	
Total	43	57	100	0.001***	119	115	234	0.020*	162	57	115	0.001***

[1] *p*-value of the Chi-square test assessing the significance of differences in the breed proportions between profiles. *($p < 0.05$); and ***($p \leq 0.001$).

Table 4
Number of cows in the four trade-off profiles according to their parity: (primiparous (1) or multiparous (≥ 2)) and to their location in the two experimental units.

Trade-off profile	Location 1: Le Pin-au-Haras			Location 2: Mirecourt			Both locations		
	1	≥ 2	*p*-Value[1]	1	≥ 2	*p*-Value	1	≥ 2	*p*-Value[1]
Profile 1	12	24		1	16		13	40	
Profile 2	22	11		39	39		61	50	
Profile 3	1	6		17	43		18	49	
Profile 4	10	14		24	55		34	69	
Total	45	55	0.001***	81	153	0.001***	126	208	0.001***

[1] *p*-value of the Chi-square test assessing the significance of differences in the proportions of primiparous and multiparous cows between profiles. ***($p \leq 0.001$).

Table 5
Percentages of dairy cows by age at first calving in the four trade-off profiles.

Trade-off profile	Age at first calving		p-Value
	2	3	
Profile 1	30%	70%	
Profile 2	50%	50%	
Profile 3	76%	24%	
Profile 4	65%	35%	
Total	57%	43%	0.001***

p-value of the Chi-square test assessing the significance of differences in reproduction success between profiles. ***($p \leq 0.001$).

significant effect on the calving-to-conception interval and reproduction success, but affected the normality of progesterone profiles. Hormonal abnormalities associated with high NEB may partly explain the fertility disorders of cows in this group. Dynamics of body reserves and reproduction performance of cows from profile 4 clearly agree with Roche et al. (2007), who showed a negative correlation between BCS loss over 84 d postpartum and a positive pregnancy outcome. However these results disagree with the findings of Roche et al. (2007) and López-Gatius et al. (2003), which showed a strong and positive correlation between BCSc and the probably of a positive pregnancy outcome or success rate at first insemination.

4.2. Individual diversity of dairy cows within trade-off profiles

We analyzed to which extend breed, parity, age at first calving or feeding level could be main factors influencing the expression of trade-off in dairy cows. One benefit of this approach was demonstrating the diversity of characteristics of individual dairy cows within each profile.

Most cows in profile 1 were multiparous (75%) (Table 4). However, 25% of primiparous cows are found in this profile, despite the fact that these cows were associated to the highest milk yields. Most cows from this profile were Holstein (77%), but a non-negligible percentage were Normande (15%) and only 3% were Montbéliarde (Table 3). These results are consistent overall, since multiparous cows are known to have higher milk yields than primiparous cows (Bruckental et al., 1989, Wathes et al., 2007), and Holstein have a higher average genetic merit for milk yield than Normande (Delaby et al., 2009). Nevertheless, our approach demonstrated that some high-yielding Normande cows, and to a lesser extent Montbéliarde cows, expressed the same trade-off profiles as high-yielding Holstein cows in early lactation. An interesting characteristic of cows in this trade-off profile is the higher percentage that first calved at 3 years of age compared to that of the population (70% vs. 43%, on average, $p < 0.001$).

Half of the cows from profile 2 were primiparous (55%, Table 4) and not from a particular breed, since the three breeds were represented in this profile in approximately the same percentages as those in the population (43% Holstein, 19% Normande and 38%

Appendix A1
Description of the set of indicators calculated to describe the dynamics of milk production, body condition and reproduction performances.

Item	Indicator	Calculation	Unit
Milk production	AMY	Average weekly milk yield	kg
	MY at peak	Highest average weekly milk yield	kg
	MYW_{13}	Average weekly milk yield in the 13th week postpartum	kg
	AMY/AMYmean	AMY divided by mean AMY of the population	
	CMP	Interval between calving and the highest average weekly milk yield	d
Body condition	BCSc	body condition score at calving	0 to 5
	N_ΔBCS < 0	The number of weeks where $BCS_n - BCS_{n-1} < 0$	
	N_ΔBCS = 0	The number of weeks where $BCS_n - BCS_{n-1} = 0$	
	N_ΔBCS > 0	The number of weeks where $BCS_n - BCS_{n-1} > 0$	
	ΔBCS (%)	BCSc − BCSweek13/BCSc	%
	BCS_{min}	Minimum body condition score	0 to 5
	BCS_{max}	Maximum body condition score	0 to 5
	ΔBCS_{min}	BCSc − BCSmin/BCSc	%
	ΔBCS_{max}	BCSc − BCSmax/BCSc	%
	ΔBCS(W2 − W1)	BCSweek2 − BCSweek1	
	ΔBCS(W13 − W12)	BCSweek13 − BCSweek12	
	$\Delta BCSW13/BSC_{min}$	$BCSweek13/BCS_{min}$	%
Reproduction	IBS1	Days open: number of days between the start date of a cow's breeding season and its 1st service	d
	IBC	Number of days between the start of the breeding season and the date of conception	d
	NS	Number of services	

Appendix A2

Correlation matrix based on Pearson coefficients, used to choose the variables included in the principal component analysis. For the abbreviation the reader can refer to the Appendix A1.

Correlations	AMY	MY at peak	MYW_{13}	AMY/ AMY_{mean}	CMP	BCSc	N_ΔBCS < 0	N_ΔBCS = 0	N_ΔBCS > 0	ΔBCS (%)	BCS_{min}	BCS_{max}	$ΔBCS_{min}$	$ΔBCS_{max}$	ΔBCS (W2 − W1)	ΔBCS (W13 − W12)	ΔBCSW13/ BSC_{min}	IBS1	IBC	NS
AMY	1	0.97																		
MY at peak	0.97	1																		
MYW_{13}	0.69	0.87	1																	
AMY/AMY_{mean}	0.76	0.76	0.67	1																
CMP	−0.08	−0.07	0.18	−0.02	1															
BCSc	0.09	0.06	0.11	−0.13	−0.01	1														
N_ΔBCS < 0	0.11	0.1	0.1	0.15	−0.01	0.2	1													
N_ΔBCS = 0	−0.08	−0.08	−0.08	−0.06	0.03	−0.18	−0.7	1												
N_ΔBCS > 0	−0.02	−0.02	−0.02	−0.12	0	−0.01	−0.29	−0.41	1											
ΔBCS (%)	−0.08	0.07	0.05	0.18	0.05	0.08	0.68	−0.29	−0.52	1										
BCS_{min}	0.06	−0.02	0.03	−0.23	−0.05	0.71	−0.3	0.13	0.23	−0.57	1									
BCS_{max}	−0.1	0.04	0.11	0.16	−0.03	0.98	0.55	0.2	0.81	0.68	0.85	1								
$ΔBCS_{min}$	0.04	−0.08	0.05	−0.17	−0.04	−0.08	−0.67	0.4	0.32	−0.94	0.63	0.81	1							
$ΔBCS_{max}$	−0.02	0.07	−0.03	−0.2	0.01	0.83	0.01	0.04	0.72	0.57	0.43	0.94		1						
ΔBCS(W2 − W1)	0.07	−0.06	−0.09	-0.07	0.02	0.67	0.72	0.03	0.14	0.49	−0.07	0.09	−0.05	0.13	1					
ΔBCS(W13 − W12)	−0.07	0.05	0.05	0.08	0	−0.56	0.71	−0.67	−0.58	0.74	−0.03	0.15	0	0.02	−0.1	1				
$ΔBCSW13/BSC_{min}$	0.02	0.06	0.04	0.16	0.04	0.07	0.66	−0.41	−0.33	0.94	−0.62	0.31	−0.99	0.41	0.06	−0.03	1			
IBS1	−0.02	−0.02	0	−0.01	0.01	−0.04	0.08	−0.01	−0.09	0.17	−0.14	0.23	0.17	−0.04	0.01	0	−0.14	1		
IBC	0.06	0.07	0.01	0.12	0	−0.14	0.1	0	−0.13	0.2	−0.21	0.25	0.18	−0.07	0.01	0.02	−0.22	0.28	1	
NS	0.06	0.07	0.05	0.06	−0.01	−0.08	−0.07	0.03	0.05	−0.05	−0.01	0.27	−0.05	0.03	0.06	0.05	−0.01	−0.12	0.43	1

Montbéliarde, Table 3). According to nutrient allocation theory, this result is biologically meaningful (Glazier, 2009). Priority rules for nutrient allocation can change in different lactation stages and parities (Yan et al., 2006). Primiparous cows from profile 2 seemed to still have growth requirements after their first calving (Lucy, 2001), contrarily to primiparous cows from profile 1, which mostly calved at 3 years of age, and which no longer seemed to require as much energy for growing, since their energy allocation was prioritized toward lactation.

Cows in profile 3 were not from a specific breed (Table 3), but most (73%) were multiparous cows (Table 4) that first calved at 2 years of age (76% vs. 57%, on average, $p < 0.001$) (Table 5). The poor reproductive performances were associated with a combination of low BCSc, an intermediate BCS loss over the study period, compared to the other profiles, independent of the breed, which is contrary to the findings of Walsh et al. (2008).

Cows in profile 4 were mostly multiparous (67%) (Table 4) and 36% were Holstein, 21% were Normande and 43% Montbéliarde (Table 3). The difference from profile 3 was the ability of profile 4 cows to maintain a relatively stable BCS during the study period. In this profile, breed does not appear a driver of the trade-off profile, even though Holstein cows were slightly less represented than Normande and Montbéliarde. These findings do not fully agree with those of Dillon et al. (2003) comparing the connection between milk yield and BCS at different lactation stages for four dairy cow breeds (Holstein, Holstein-Friesian, Montbéliarde and Normande).

Looking at the distribution of Normande and Montbéliarde cows over the different trade-off profiles, we observed an over-representation in the profile 2 and 4. This is again questioning the finding of Dillon et al., (2003) who showed that Normande cows experienced the least variation in BCS during the entire lactation period closely followed by Montbéliarde cows, with particularly significant differences during the first 8 weeks of lactation. Indeed, in our study cows from profile 2 recorded the largest body reserves mobilization of the studied period.

We demonstrated that trade-offs expressed by dairy cows are not only driven by milk yield, breed or parity, since cows of each breed and parity were encountered in all four trade-off profiles and since profiles 3 and 4 did not differ in lactation function (Tables 4 and 5). These results agree with those of Horn et al. (2014), who showed no effect of cow breed (Brown Swiss vs. Holstein) on milk production, reproduction and BCS in response to nutritional challenges. These results challenge the normative procedures requiring that cows be separated by breed and parity when studying their metabolic functions or responses to challenges (Dillon et al., 2003, Delaby et al., 2009, Horan et al., 2006, Horn et al., 2014 and Yan et al., 2006). Diversity in dairy cow trade-off expression does not seem predictable from only the main individual characteristics. The energy level of the diet influenced trade-off expression in profiles 1 and 2. Cows from profile 1 were mostly fed a high energy diet (L-HED, M-HED or M-MS) (89% vs. 69% on the average), and cows from profile 2 were fed mostly a low-energy diet (L-LED or M-GS) (48% vs. 31%, on average). For profiles 3 and 4, energy level of the diet had no significant effect on distribution of cows among profiles. Differentiation of high milk yields was associated with a high feeding level in profile 1, and low milk yields were associated with a low feeding level in profile 2. Thus, the nutritional environment seems to affect trade-off expression when cows are able to modulate energy allocation to lactation: prioritize lactation in profile 1, neglect lactation in profile 2.

This is of biological interest and highlights the need to better understand mechanisms that drive nutrient-allocation prioritization. The effect of the environment is also important. Interactions between genotypes and the environment should be explored over the long term to fully understand the expression of trade-off phenotypes (Friggens and Newbold, 2007). This multi-trait clustering approach constitutes a support method to further investigate trade-offs between functions in dairy cows by using existing datasets.

4.3. Possible uses for the multi-trait clustering approach

This multi-trait approach was inspired by recent genetic selection that integrates functional traits into breeding programs (Calus et al., 2013). This shift is an important step for the future of animal selection (Amer, 2011). Nevertheless, transposing this method to selection tools would require high-throughput phenotyping data on lactation, body condition and female reproduction followed by breeding organizations. In addition, some of the indicators used in this study can be improved to better describe the dynamics of responses. Specifically, accuracy of assessments of body reserve dynamics is to be improved, for instance, by replacing BCS traits with measurements of β-hydroxybutyrate in milk (Bernabucci et al., 2005), which can be assessed more frequently and better reflects health status of the cow. Mid-infrared analysis is a relevant tool for obtaining more precise representation of temporal changes in energy status with higher sensitivity (Berry et al., 2013; McParland et al., 2015), shorter time-steps and greater reliability (Bewley and Schutz, 2008) than BCS estimates. It would also be one way to consider the metabolic health status of cows in our approach.

Berry et al. (2013) used extent and duration of NEB as a proxy for robustness measurements to assess robustness in dairy cows. Our approach demonstrated that the only measure of NEB does not appear sufficient to discriminate the trade-off profiles of cows in our dataset. We suggest combining our multi-trait approach with the precise NEB measurements and assessment of body-reserve mobilization developed in the ROBUSTMILK project. This could provide a new perspective for evaluating robustness in dairy cows that explicitly and simultaneously accounts for multiple functions of interest. Also, as suggested by Calus et al. (2013), coupling our approach with genomic selection could provide an efficient way to study the relatedness and variability of phenotypic expression of trade-off in a large population of dairy cows.

This multi-trait clustering approach could also be implemented in studies that describe dairy cows' adaptive responses to disturbances (Friggens et al., 2013). When an animal experiences stressors, phenotypic plasticity may occur, and reorganization of nutrient-allocation priorities among life functions could be an adaptive strategy (Friggens and Newbold, 2007). Thus, using this new approach could help obtain greater insights into dairy cows' adaptive strategies and characterize genotype × environment interactions.

These trade-off profiles could also provide new management tools for farmers. Puillet et al. (2010) demonstrated the role of individual variability on herd performances and responses to management. Therefore, there is real value in analyzing the diversity of trade-off expression when deciding on herd composition. Associating complementary trade-off profiles, including milk production, BCS elasticity and ability to reproduce, could provide indicators to farmers to help them adapt the composition of their herds according to their management practices, production objectives, the exposure of their livestock to disturbances, and the availability of feed resources (grazing vs. indoor rearing, seasonal calving vs. spread calving, targeted levels of production, etc.). As suggested by Delaby and Fiorelli (2014), spreading the calving of the herd into two main breeding seasons is a feasible option for farmers to optimize the use of forage resources. Similarly, it may be possible to adjust the reproductive management of cows according to their trade-off profiles. In low-input systems, cows from profiles 2 and 4 could be managed to create a short calving period in the spring to optimize the use of grass. The reproductive period of cows in profiles 1 and 3 could be more flexible, with mostly autumn and winter calving, to spread milk production over the year and reduce the risk of a major loss of production in the event of unpredictable disturbances affecting forage availability.

5. Conclusions and perspectives

This multi-trait clustering approach represents an operational tool to assess trade-offs between life functions in dairy cows. Four main trade-off profiles were obtained that rely on a combination of milk yield, stability of body condition score and reproductive performances. The diversity of trade-off phenotypes highlighted by our approach better represents the diversity that exists in expression of nutrient partitioning priorities. Regarding dairy cow selection programs, integrating these trade-off profiles could help assess animal robustness in light of characteristics of the livestock-production system. This approach could be used to explain and perhaps plan adaptive responses to disturbances. High-throughput phenotyping data collected in a variety of farm environments are needed to further improve and validate this multi-trait clustering approach. In addition, more studies are needed to record the evolution of trade-off expression over the lifespan of individual dairy cows. Finally, the diversity of trade-offs expressed by cows emphasizes the utility for farmers to consider dairy herd composition and optimize its consistency with their objectives and the farm environment.

Conflict of interest

No conflict of interest is to be disclosed according to the information provided at http://www.elsevier.com/journal-authors/author-rights-and-responsibilities.

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Appendix A

See Appendix Table A1 and Table A2

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