Lohmann Information

Use of L-carnitine additions in domestic animal feeds

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1 Introduction

To investigate the effects of L-carnitine supplementations in domestic animal feeds an increasing number of trials have been performed in different domestic animal species and under different production areas. The purpose of this survey is to collate some available information which appeared to be pertinent to this subject. With respect to literature this survey is not complete. The author tried to address the present situation and to highlight and discuss trends in the current use of dietary L-carnitine.

The available data are organized according to animal species, starting with horses and ending with racing pigeons. Information from other species have been included when this appeared reasonable.

2 L-carnitine status

Dietary supplements of L-carnitine at dose rates of 20 to 500 mg/kg feed, depending on indication, raise plasma L-carnitine levels in domestic and laboratory animals including birds and fishes (LaCOUNT et al., 1995; FOSTER and HARRIS 1989a, b; NEGRAO et al., 1987; NEGRAO et al., 1986; WEEDEN et al., 1990). The concentration increases can be 100 % or more depending on the dosage. When administering L-carnitine to ruminants it is advisable to use "rumen protected" preparations since rumen microbes degrade L-carnitine relatively quickly. Moreover, the degradation rate of L-carnitine in the rumen increases with the duration of supplementation (LaCOUNT et al., 1996b; HARMEYER and SCHLUMBOHM, 2001). L-carnitine administered to ruminants in an unprotected form is no longer detectable in the rumen 12 to 4 hours later, depending on the duration of supplementation. Absorption of L-carnitine through the rumen wall can be ruled out (own findings). Oral L-carnitine supplements also increase the L-carnitine content in animal products such as eggs (LEIBETSEDER, 1995), milk (KAISER, 1997; BENAMOU and HARRIS, 1993) and lean muscle (IBEN and MEINART, 1997; BENEVENGA et al., 1989; NEGRAO et al., 1987). In these products, too, the L-carnitine concentration can rise by up to 100 % above the control value. This usually requires supplementation over a period of several weeks.

3 Domestic animals

3.1 Athletic horses

Studies were carried out with race horses and breeding mares to examine the effect of L-carnitine on exercise performance or reproductive functions. Oral supplementation of 5 to 20 g of L-carnitine/d was used and was applied for several weeks. When L-carnitine additions were combined with physical training, the L-carnitine supplementation reduced the exercise-induced increase of blood lactate and the exercise-induced increase of non-esterified free fatty acids in plasma. These effects were interpreted as beneficial with regard to exercise performance. In another experiment addition of 2 x 10 g L-carnitine/day reduced the concentration of triglycerides and of non-esterified free fatty acids (NEFA) in the plasma. The plasma glucose concentration rose (HAUSENBLASZ et al., 1996). Another question asked, in this context, was, whether additions of L-carnitine might influence the L-carnitine content of the skeletal muscle? In own experiments in which two year old trotters were orally supplemented with 10 g L-carnitine/d for 5 weeks combined with an exercise training programme, the content of total L-carnitine in resting glutaeal muscle was elevated by 46 % (COENEN et al., 2000; HARMEYER et al., 1999). In other experiments, administration of L-carnitine to lactating mares alleviated the sharp fall of plasma L-carnitine in suckling foals during the early weeks of lactation (BENAMOU and HARRIS, 1993). More aspects about effects of L-carnitine supplementation of horses have been reviewed elsewhere (ZEYNER and HARMEYER, 1999).

3.2 Cows and cattle

Experiments have been carried out in cattle in which metabolic and performance effects of L-carnitine additions were investigated. It is of interest to note that the ruminant liver possesses a much lower capacity for biosynthesis of fatty acids (BALLARD et al. 1969, BRINDLE et al. 1985) and for synthesis and secretion of lipoproteins (VLDL) (HOCQUETTE and BAUCHART, 1999) than the liver of non-ruminant species. Despite this difference, it appears that L-carnitine also plays an important role in ruminant liver function. Inhibition of palmitoyl transferase I activity (CPTI) by malonyl CoA (an intermediate of fatty acid biosynthesis from acetyl-CoA), for example, is as effective in sheep liver as it is in liver slices from non-ruminant species (BRINDLE et al., 1985).

In dairy cows, mitochondrial CPTI activity was higher during lactation than during the non-lactating state. The activity of this enzyme decreased in dairy cows with development of a fatty liver (MIZUTANI et al., 1999; AIELLO et al., 1984). Addition of L-carnitine to liver slices of lactating and non-lactating cows more than doubled the rate of palmitate oxidation and significantly lowered esterification rate of palmitate to triglycerides (DRACKLEY et al., 1991a; DRACKLEY et al., 1991b) which showed the essential role of L-carnitine for fatty acid oxidation in ruminant liver. Therefore, it is not surprising that the content of liver L-carnitine is influenced by the composition of diet. Pregnant cows were fed either a high energy fat or an isocaloric high energy grain diet (GRUM et al., 1996). The cows which received the high fat diet had a lower triglyceride content and a higher concentration of acid soluble L-carnitine in the liver during the last 3 weeks pre-partum than cows receiving the high energy grain diet.

In the blood of dairy cows the concentration of L-carnitine decreases with the onset of lactation (FÜRLL et al., 1999; SNOWSWELL and LINDSELL, 1975). This probably reflects the sudden increase in L-carnitine excretion with the beginning of lactation. The concentration of L-carnitine esters significantly increases in cows' milk and blood plasma with onset of subclinical or clinical ketosis compared to milk and plasma from non-ketotic cows (FÜRLL et al., 1997; ERFLE et al., 1974). This demonstrates that L-carnitine probably binds to activated acyl moieties in the presence of high amounts of fatty acid degradation products forming L-carnitine esters. In dogs, L-carnitine supplementation significantly alleviated the symptoms of acute, life-threatening acidosis and ketosis induced artificially through lipid perfusion (BROCKHUYSEN et al., 1965).

Part of the L-carnitine which was given to ruminants with feed was probably degraded in the rumen and the rate of degradation of L-carnitine in the rumen increased with

time of feeding L-carnitine (LaCOUNT et al., 1996b; own observations). Obviously, some L-carnitine escapes rumen degradation when free L-carnitine is administered to the rumen. The L-carnitine concentration in plasma and liver increased to about the same extent when a certain dose of L-carnitine was administered either into the rumen or directly into the abomasum (LaCOUNT et al., 1995). However, in own experiments with fistulated sheep it was found that the L-carnitine concentration in plasma was significantly more elevated when L-carnitine was infused into the abomasum rather than into the rumen (unpublished). In addition, when the supplemented L-carnitine was infused into the omasum rather than into the rumen, the concentration of L-carnitine in blood plasma and urine increased linearly with the infused dose of L-carnitine, with doses up to 6 g/day (LaCOUNT et al., 1996a). After omasal administration of L-carnitine its concentration in milk increased quadratically which probably shows that the mammary gland effectively extracts L-carnitine from blood plasma and secretes it into milk. A positive correlation exists between the milk fat content and the content of L-carnitine in the milk (ROOS et al., 1992).

Possible effects of oral L-carnitine supplementation to growing and finishing steers have also been examined (GREENWOOD et al., 2001). The studies showed that in L-carnitine supplemented animals (2 g L-carnitine/d), the concentration of non-esterified free fatty acids decreased before feeding and increased after feeding. Blood glucose tended to increase during L-carnitine supplementation. The addition of L-carnitine had no effect on average daily gain and feed conversion ratio (GREENWOOD et al., 2001). However, it must be taken into account that, under these conditions, the ruminal escape of the administered L-carnitine might have been low and the amount of L-carnitine available to the host animal might have been too small to affect performance parameters of the steers.

3.3 Sheep

As outlined for cows, oral administration of L-carnitine also elevated plasma glucose concentration in growing sheep (CHAPA et al., 2001). In another study with sheep, three groups of merino lambs were fed for 49 days 0, 100 or 200 mg of L-carnitine/d. L-carnitine supplementation exerted no effect on feed intake or live weight gain (PETEK and DINIZ, 2000). Again, it appears that the orally applied amounts of L-carnitine were probably too small to exert a metabolic effect in the merino sheep. In another series of experiments with growing sheep, it was repeatedly shown that higher amounts of L-carnitine reduced the ammonia concentration in blood after experimentally induced hyperammonemia. The significant effect of L-carnitine in lowering blood ammonia was documented after oral urea loads (CHAPA et al., 2001). The protective effect was greater when L-carnitine was intravenously injected about 1/2 hour before the oral urea drench instead of applying it orally (CHAPAET al., 1998). Protective effects of L-carnitine against induced ammonia intoxication have also been reported from man (BOEHLES et al., 1996; FELIPO et al., 1994) and rats (GAZOLA et al., 2001). This property of L-carnitine to protect against ammonia intoxication may perhaps be of interest in fattening cattle under condition of non-protein nitrogen feeding. Such a feeding regime implies the risk of high rates of ammonia formation in the rumen.

3.4 Pigs

The possible effectiveness of L-carnitine in pig husbandry has, in comparison to some other species, received much attention. Quite a few publications have appeared which quote the positive effects of L-carnitine on growth performance, carcass composition and/or breeding parameters.

- **Boars**

Seminal and epididymal plasma of domestic animals and rodents contain remarkably high values of L-carnitine (JONES, 1978; HINTON et al., 1979; CARTER et al., 1980). In the fluid from boar ductus deferens a total L-carnitine concentration of 22 mmol/l was measured and the corresponding concentration in ductus deferens fluid from rats was 53 mmol/l (BROOKS et al., 1974). These concentrations were about 630 to 1500 times that in blood plasma. This constitutes perhaps the highest concentration of L-carnitine in body fluids. The L-carnitine is not synthesized by the epididymal tissue but is taken up from blood plasma by a mechanims which are under androgenic control (BØHMER and JOHANSEN, 1978). Provided this amount of L-carnitine dissolves freely in the aqueous phase of the fluid, it would contribute to the osmotic pressure with 137 and 329 mosm/l, respectively. The concentration of total L-carnitine in epididymal fluid progressively increases during its transit from proximal to caudal, i.e. from the caput through the corpus to the cauda epididymis (DACHEUX and PAQUIGNON, 1980). The increase in L-carnitine concentration is parallelled by maturation of the spermatozoa which includes an increasing ability to move and to fertilize (JEULIN et al., 1988; JEULIN et al., 1987; DACHEUX and PAQUIGNON, 1980). L-carnitine is taken up by epididymal spermatozoa from the epididymal fluid by passive diffusion. The L-carnitine concentrations in the epididymal fluid and in the spermatozoal plasma equilibrate (JEULIN et al., 1994). This results in a continuing increase in the concentration of free L-carnitine in the spermatozoa as they pass down the epididymal duct.

Oxidative metabolism of spermatozoa also increases during transit through the epididymal duct from caput to cauda epididymis (DACHEUX and PAQUIGNON, 1980). This is associated with an increase in the carnitine acetyl transferase activity and an increasing capacity of the spermatozoa for acetylation of free L-carnitine. In caput spermatozoa the capacity for free L-carnitine acetylation is small (JEULIN et al., 1994). Acetyl-L-carnitine accumulates in spermatozoal plasma of cauda spermatozoa, since the permeability of the spermatozoal plasma membrane of maturing spermatozoa for acetyl-L-carnitine is much less than for free L-carnitine (JEULIN et al., 1994). It appears that spermatozoa acquire the ability to accumulate L-carnitine and in particular acetyl-L-carnitine while they mature. It is believed that acetyl-L-carnitine in spermatozoa serves as a readily accessible energy pool which is used for ATP production in respiration and motility (JONES and BUBB, 2000, HINTON et al., 1979). Unusually low concentrations of L-carnitine in spermatic fluid may indicate poor sperm quality, poor fertility and an impaired epididymal function.

- **Reproducing sows**

In an attempt to examine the effect of L-carnitine in reproducing pigs, 60 sows were supplemented with 125 mg of L-carnitine/d during pregnancy and with 250 mg/d during lactation (EDER et al., 2001). In this study the supplemented sows gained significantly more weight between d 1 and d 85 of gestation. Mean birth weights of piglets and mean litter weights were 6 to 9 % higher compared to non-supplemented control animals. The higher litter weight of the piglets from supplemented sows was maintained post weaning. L-carnitine showed no effect on litter size in this study.

In another experiment, L-carnitine was administered with feed to 207 sows during pregnancy and lactation in different concentrations which ranged from zero to 200 mg/kg feed (MUSSER et al., 2000). The number of piglets born from sows fed 50 mg L-carnitine per kg was larger than that from control sows. Analysis of the semitendinosus muscle from new-born piglets indicated a larger cross-sectional area and more total muscle fibres in piglets from sows fed with added L-carnitine. On the other hand, it is of interest to note that, in earlier experiments partly carried out by the same authors, by use of larger numbers of sows, additions of 50 to 200 mg of L-carnitine/kg feed during pregnancy and/or lactation showed no effect on sow and litter performance (MUSSER et al., 1997a; MUSSER et al., 1999).

In still another experiment in which 307 sows were supplemented with 100 mg of L-carnitine/d during gestation and with 50 mg/d during lactation, supplementation with L-carnitine resulted in a positive response (MUSSER et al., 1997b). The sows fed L-carnitine had increased body weight, increased last rib fat depth and an increased concentration of the anabolic hormone insulin-like growth factor I (IGFI) in blood plasma. In this study the offspring also responded positively to the supplementation of L-carnitine. Total litter weights at birth, litter weights at weaning and pig weights, were all increased.

Improvement of reproductive performance of sows was also observed in another investigation in which 50 mg of L-carnitine/kg feed was given together with 200 g of chromium picolinate (Carnichrome®) (LOPEZ, 2001). This preparation appeared to improve farrowing rate and percentage of non-return to oestrus in the sows, but showed no influence on the number of pigs born alive. Surprisingly, addition of L-carnitine alone (without chromium) showed no effect in this study.

Inclusion of 120 mg carnitine per kg feed and its administration to pregnant sows from 4 weeks ante partum to weaning of the piglets increased the concentration of free carnitine in sow plasma during the period from two weeks before to two weeks after farrowing by 24 and 73 % respectively compared with controls (Figure 1). In the non-supplemented group of sows the total carnitine content in the plasma fell by 25 % from two weeks ante partum to two weeks post partum. This decline was offset by the carnitine supplement. The content of total carnitine in the milk was raised through supplementation by 60 % on the first day of lactation and by 39 % at the end of the second week of lactation (Figure 1). The total carnitine content in sows milk declined by 42 % in the first two weeks of lactation, irrespective of the carnitine supplement (Figure 1). However, its concentration was always higher in the milk of the supplemented sows than in milk of the non-supplemented sows. As a result of adding carnitine to the sows ration (120 g/kg) the concentration of total carnitine in the plasma of the piglets rose by 100 % compared with the non-supplemented group of piglets. This was primarily due to a continuous increase in free carnitine over a 3-week period. The free carnitine in the control piglets remained approximately constant during this time (Figure 2).

Figure 1: Content of total L-carnitine in milk (top) and plasma (bottom) of sows with and without L-carnitine supplementation ($\bar{x}$ ± SD, N = 14)

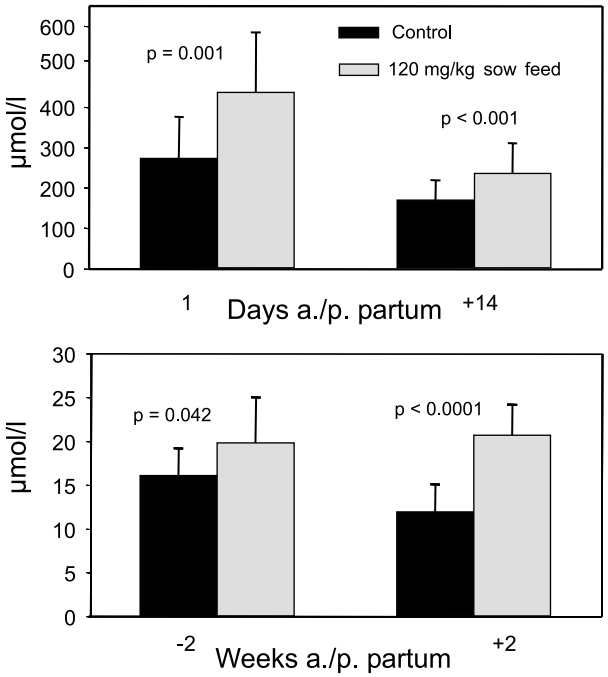
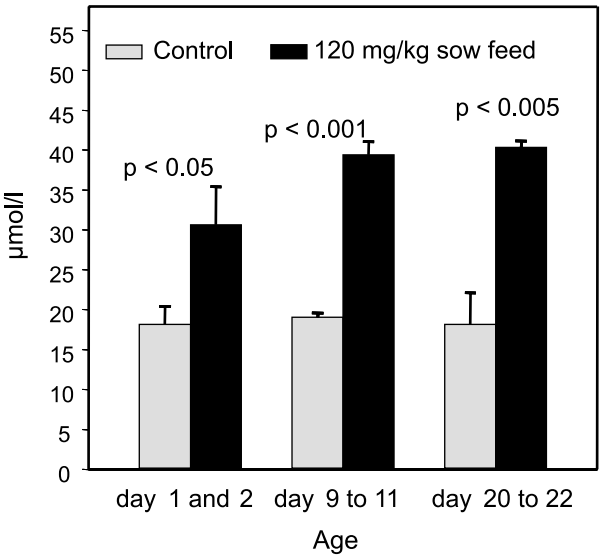


Figure 2: Content of total L-carnitine in plasma of piglets at 1 to 22 days of age (sow ration with and without supplemental L-carnitine ($\bar{x}$ ± SD, N = 14)



- **Nursery pigs**

It is well documented that new born and suckling piglets require external L-carnitine which normally comes from colostrum and sows' milk. This has been demonstrated by an experiment in which 2 weeks old suckling piglets were switched for one week from suckling to L-carnitine-free total parental nutrition (TPN). The L-carnitine content in blood, liver and heart drops significantly during this time (PENN et al., 1997). During TPN the L-carnitine-deprived piglets showed evidence of lipid deposition in the liver and skeletal muscles. They had a higher incidence of muscle weakness and cardiac failure than control piglets which received L-carnitine-supplemented parenteral nutrition during this time. Further support for the view that new-born piglets require external L-carnitine can also be obtained from findings that blood and liver of piglets show low concentration of total L-carnitine at birth. The L-carni-

tine concentration increases 2 to 4-fold after 2 days of suckling (KERNER et al., 1984). The total L-carnitine content of sow's colostrum was estimated to be 370 µmol/l with 95 % being acylated (KERNER et al., 1984). The L-carnitine content gradually decreases in sow's milk with time of lactation (LI et al., 1992). L-carnitine concentration in sow's milk is more than ten times higher than that present in the blood of the piglets. In the blood of the piglets, however, about 90 % of total L-carnitine is free L-carnitine.

Positive effects on daily gains during piglet rearing (LITZ, 1993) were observed in feeding regimes where the content of methionine or lysine in the basal ration was limited. This deficiency seems to reduce endogenous carnitine synthesis. Under these circumstances the L-carnitine supplement was, however, only partially able to offset the growth depression caused by the amino acid deficiency. If there is evidence of a slight deprivation in the dietary concentrations of lysine and methionine, L-carnitine supplementation is likely to prove beneficial.

In orphan or early weaned piglets an appropriate L-carnitine supplement added to the milk replacer as a substitute for the high L-carnitine content of sows milk is definitely advisable and beneficial (AERTS and FREMAUT, 1996; AERTS et al., 1992). The L-carnitine content in milk replacer should be higher than the L-carnitine content in sows milk because in mammals native L-carnitine from maternal milk leads to a greater increase in the plasma L-carnitine concentration than the same amount of L-carnitine administered as a supplement in milk replacer (WARSHAW and CURRY, 1980).

A number of feeding trials were carried out with piglets in which the dosage of L-carnitine was comparably high. Supplementation of L-carnitine at concentrations of 250 to 1,250 mg/kg feed to nursery piglets from d 23 to d 35 showed no effect on growth and percentage of carcass crude protein, lipids and protein accretion (OWEN et al., 2001a). The rate of lipid accretion, however, tended to decrease. Another earlier study involved a similar experimental set-up (OWEN et al., 1994a; OWEN et al., 1994b). In this study no marked influence of L-carnitine was observed on average daily weight gain and on feed intake. However, the pigs fed 1.000 mg L-carnitine/kg feed in this trial were heavier on d 35 than pigs on control treatment. Daily fat accretion rate was also reduced in another trial by the same authors with piglets which received L-carnitine up to 750 mg/kg feed. Finally, another growth trial was performed, partly by the same authors. In this experiment a total of 300 weaning piglets were administered L-carnitine at dosages of 500 and 1,000 mg/kg feed from d 0 to d 14 post-weaning and at dosages of 250 and 500 mg/kg from d 15 and d 35 (OWEN et al., 1996a). In this trial a decrease in average daily feed intake and an increase in feed/gain ratio was recorded in the L-carnitine-supplemented groups from d 15 to d 35. However, some of the L-carnitine-supplemented groups of pigs had again less carcass lipid and a lower lipid accretion rate at d 35 post-weaning than control pigs which received no L-carnitine. One may speculate whether the dosages of L-carnitine used in these latter studies were perhaps too high to produce positive effects on growth (see below). Nevertheless, in several more recent Korean studies nursery pigs were fed with 500 and 1,000 mg L-carnitine/kg feed (CHO et al., 2000; CHO et al., 1999a; CHO et al., 1999b). The L-carnitine additions improved the digestibility of dry matter and crude protein, increased N-retention and improved average daily gain and gain:feed ratio.

An equally positive response was also obtained with weaned piglets (35 d) with 50 mg of added L-carnitine/kg feed after a supplementation period of 6 weeks (LI et al., 1999). In this trial the positive response of the pigs to the added L-carnitine was independent from the fat content of the diet (± 5 % soybean oil or ± 5 % lard). In yet another experiment in which amounts of 50 or 150 mg L-carnitine/kg feed were given to nursery piglets for 30 d, no effect of L-carnitine was seen on growth, feed intake and feed conversion (PIAO et al., 2000). However, in this trial the 21 d old piglets were fed an extruded full-fat soybean diet to which the young animals could not fully adapt. This latter study probably shows that when the basal diet is inadequate the addition of L-carnitine produces no improvement. In many trials additions of L-carnitine to pig starter feed used from about 4 to 9 weeks post weaning at concentrations of 25 or 50 mg/kg feed showed positive effects on feed conversion (GALVEZ et al., 1996; JOST and BRACHER-JACOB, 1996; JOST and BRACHER-JACOB, 1994) and less consistently positive effects on daily gain (SCHÖNE et al., 1991). Negative results, however, are also reported (BERK et al., 1999).

Summarizing these results it appears that additions of high doses of L-carnitine to pig diets are of relatively little value to the piglets. In some of the studies such high dosages of L-carnitine seemed to have exerted negative effects on performance characteristics. From the present body of information it appears difficult to derive clear dose/response relationships with L-carnitine. It, would therefore be of interest to know whether such dose/response relationships exist for L-carnitine and whether they may vary with age of the pigs.

- **Grower and finisher pigs**

Positive effects of L-carnitine supplementation were also observed in growth and metabolic trials with pigs during the grower and finishing period. In a 10 d N-balance study with 25 growing pigs (18 kg BW) supplementation of 500 mg L-carnitine/kg feed increased average daily gain (7.3 %), crude protein accretion rate (9 %), N-retention and L-carnitine accretion rate (4 to 5-fold) (HEO et al, 2000a; HEO et al., 2000b). In another trial with 96 animals, the effect of high doses (from 250 to 1,250 mg/kg feed) and low doses (from 25 to 125 mg/kg feed) of L-carnitine as a feed supplement was tested in grower and finisher pigs (OWEN et al., 2001a). The trial showed that the high doses of L-carnitine had no effect on growth, percentages of carcass crude protein, lipid or daily protein accretion. The low doses of dietary L-carnitine decreased average and tenth-rib back-fat and increased the percentage lean and daily protein accretion rate. From statistical analysis it appeared that the most effective dosage of L-carnitine for influencing these traits appeared to be between 49 and 64 mg/kg feed. The findings were in accord with those from earlier experiments (OWEN et al., 1994c; OWEN et al., 1996b; OWEN et al., 1994c) with similar experimental set-ups, which had also shown positive effects of L-carnitine on muscle deposition, reduction of fat accretion and average and tenth-rib back-fat depth preferentially, with dosages of 50 mg/kg feed.

Most effective dosage level

From an economic point of view it is of principal interest to know what the most effective dosage of L-carnitine is, that will be required to exert the desired effects. Some experiments with different dosage levels of L-carnitine

Table 1: Survey of experiments comparing different dietary dosages of L-carnitine in pig diets

Experimental period	No. of animals	Dosages of L-carnitine (mg/kg feed)	Author
Sows during gestation	Exp. 1 66 sows Exp. 2 141 sows	0, 50, 100, 200 0, 50, 100, 200	MUSSER et al. (2000)
Sows during gestation and lactation	different experiments total No. 272	0, 50, 100, 200	MUSSER et al. (1999)
Weaned piglets, 0-35 d after weaning	Exp. 1 120 piglets Exp. 2 180 piglets	0, 500, 1000 0, 250, 500, 1000	OWEN et al. (1996a)
Weaned piglets 4-9 weeks post-weaning	84 piglets	0, 25, 50	GALVEZ et al. (1996)
Weaned piglets for 5 weeks post-weaning	128 piglets	0, 25, 50	JOST and BRACHER-JACOB (1994)
Weaned piglets for 5 weeks post-weaning	128 piglets	0, 25, 50	JOST and BRACHER-JACOB (1996)
Weaned piglets starting weight 8 kg	168 piglets	0, 50	BERK et al. (1999)
Nursery piglets, 21-35 d	216 piglets	0, 250, 500, 750, 1250	OWEN et al. (1994b)
Nursery piglets	80 piglets	0, 50, 100, 150	PIAO et al. (2000)
Nursery piglets	Exp. 1 216 piglets	0, 250, 500, 750, 1250	OWEN et al. (2001a)
Growing, finishing pigs	96 pigs	0, 25, 50, 75, 100, 125	OWEN et al. (1994c)

have been carried out to determine this. The L-carnitine doses used in these studies ranged from 25 (OWEN et al., 1994c) to 1,250 mg/kg feed (OWEN et al., 2001a) (Table 1). Unfortunately, most of these trials provided no clear dose/response relationship for the parameters under investigation. The experiments repeatedly showed, however, that dietary levels of L-carnitine around 50 mg/kg feed were, in general, more effective than higher or lower dosages (OWEN et al., 1997). In addition, it appeared that L-carnitine supplementations > 250 mg/kg sometimes exerted adverse effects on feed intake and growth. The reason for this observation is still unclear.

How can the positive effects of L-carnitine in animal production be explained?

Under in vitro conditions, additions of L-carnitine usually stimulate degradation of fatty acids. This also applies to pig tissues. For example, in isolated heart and liver tissues from 15 h non-suckled piglets, addition of L-carnitine increased oxygen consumption in the presence of palmitoyl-CoA and doubled the rate of palmitoyl-CoA utilization (HONEYFIELD and FROSETH, 1991). This observation is in accord with the known carrier function of L-carnitine in the transport of acyl-CoAs across the inner mitochondrial membrane. This is, however, no proof that L-carnitine constitutes a limiting factor for utilization of acyl-CoA, also in vivo. Experiments from HEO et al. (2000c) indicated that this might in fact not be the case. The authors 2000c showed that the Michaelis-Menten constant Km of the L-carnitine palmitoyl transferase I (CPTI) in the liver of young pigs (but not in skeletal muscle) increased when the animals were supplemented with L-carnitine. This finding indicates that the affinity of CPTI to L-carnitine is lowered when its concentration increases. This would keep the enzyme function constant. The pigs used in the experiment received the comparatively large amount of 500 mg of L-carnitine/kg BW. In any case the finding showed that the activity of the hepatic CPT I is under regulatory control and that its affinity to L-carnitine may be modified when the available amount of L-carnitine is changed. From this and other findings, it may be speculated that the positive effects of L-carnitine additions on parameters of production performance may not be mediated by the classical catalytic and/or metabolic functions of L-carnitine. In this context it is of interest that pregnant sows receiving 100 mg of L-carnitine/kg feed had increased concentrations of insulin-like growth factor I (IGFI) at d 60 and d 90 of gestation (MUSSER et al., 1997b). The frequently observed effect of L-carnitine additions to feed of pigs of increasing percentages of lean and muscle and decreasing backfat thickness can perhaps be attributed to the increased assimilation rate of methionine and to a decreased rate of branched-chain a-ketoacid degradation which was observed in isolated hepatocytes from pigs supplemented with L-carnitine (OWEN et al., 2001b).

3.5 Poultry

Effects of dietary L-carnitine additions have also been examined in broiler chicken and laying hens. The doses of L-carnitine which were applied in this species ranged from 50 to about 150 mg/kg feed. In broilers L-carnitine supplementation of 20 to 100 mg/kg feed improved average daily gain by about 2.5 % (LETTNER et al., 1992; IBEN and MEINHARDT, 1997). In another trial no effect of 100 and 200 mg of L-carnitine/kg feed was observed on growth (BUYSE et al., 2001; LEIBETSEDER, 1995).

However, as in pigs, 100 mg of added L-carnitine/kg feed lowered abdominal fat content at low environmental temperatures and significantly elevated proportional heart weights (BUYSE et al., 2001). On this evidence, L-carnitine was regarded as a potential agent for reducing the incidence of metabolic diseases in broiler chicken. Definite positive effects on weight gain, feed conversion and meat/fat ratio of individual muscles were obtained in broiler chicken by addition of 50 mg of L-carnitine/kg feed in the study of RABIE et al. (1997 a, b). The added dose of L-carnitine also resulted in a significant decrease of the abdominal fat content. No effect of 50 and 100 mg L-carnitine/kg feed on growth and body fat content was reported in an earlier study, irrespective of the fat content (1 and 5 %) of the diet (BARKER and SELL, 1994). Absence of an effect of 30 and 160 mg L-carnitine/kg feed on growth performance and carcass characteristics was also reported in broiler chicken by RICHTER (2002) and LIEN and HORNG (2001), respectively. In the study of LIEN and HORNG the added L-carnitine showed marked effects on serum composition, leading to a lower triglyceride content and a lower concentration of non-esterified fatty acids. The L-carnitine content of broiler muscle ranges from 40 to 80 mg/kg wet weight (own observations). It would perhaps be of interest to test whether the L-carnitine content of broiler feed affects the lysine requirement of the fast growing chicken.

Addition of 50 and 100 mg of L-carnitine/kg feed significantly increased hatching rates of broiler chicken (LEIBETSEDER, 1995) and increased the proportion of egg albumen at the expense of yolk (RABIE et al., 1997 c). It is also of interest to note that supplementation of broiler feed with 100 mg L-carnitine/kg may act as an immune modulator by increasing the total Ig and IgG levels in 2 to 6 w old animals (MAST et al., 2000). The immune responses were measured following immunisation with bovine serum albumin.

3.6 Pigeons

According to a number of publications, mainly from a group in Gent (Belgium), it appears that benefits affecting reproduction and physical performance from L-carnitine addition may be expected in racing pigeons. For example, in trained racing pigeons, oral supplementation of 90 mg L-carnitine for one week led to an improved fatty acid oxidation (JANSSENS et al., 1998a) and an improved energy usage (JANSSENS et al., 1998b) during heavy exercise, induced by electrostimulation of breast muscle. In females, oral additions of L-carnitine before flight may result in higher weight losses which are, however, usually compensated for by larger nutrient intakes by the supplemented animals (JANSSENS and De WILDE, 1995a). Zootechnical performance was also improved over several breeding rounds by continuing oral supplementation of 80 mg of L-carnitine/d. The added L-carnitine increased nutrient intake (JANSSENS and De WILDE, 1994) and body weight or decreased weight losses (JANSSENS and De WILDE, 1995b) of parent birds. It also increased body weights of squabs, increased crop milk production and L-carnitine content in plasma and in crop milk of parent pigeons (JANSSENS et al., 2000a; JANSSENS et al., 1999b). The L-carnitine content was also increased in breast muscle of squabs (JANSSENS et al., 2000a; JANSSENS and De WILDE, 1994). The dietary L-carnitine did not prevent weight loss in pigeons which were put from a high on to a low energy diet (JANSSENS et al., 1999a). L-carnitine additions lowered the plasma concentration of NEFA and reduced a performance-induced increase in NEFA and lactate (BORGHIJS and De WILDE, 1992).

As reported for broiler chicken, L-carnitine also increased the immune response in adult pigeons induced by parenteral administration of bovine serum albumen (JANSSENS et al., 2000b).

4 Summary and conclusions

1. The growing number of feeding trials with supplemented L-carnitine which have been carried out with various domestic animal species, including horses, dairy cows, fattening cattle, sheep, pigs, poultry and pigeons have added knowledge about effects of such additions under different conditions of animal production. Attention was given to the following findings.
2. Dietary supplementations of L-carnitine improved **reproductive performance of sows** by increasing litter size, mean birth weights, and mean litter weights. This was observed in many but not in all trials. In some trials additions of L-carnitine to **pig starter diets** improved gain to feed ratios. A similar effect was observed in pigs during the **growing and finishing period**. The dosages of L-carnitine which were applied in these studies ranged from 25 to 1,250 mg per kg feed. It appeared from the experiments that in most cases L-carnitine levels higher than 50 to 100 mg per kg were of little benefit to the animals.
3. Positive effects of dietary additions of L-carnitine were reported in trials with **laying hens** and **broiler chicken**. L-carnitine supplementations increased hatching rates, proportion of egg albumen at the expense of yolk; in broiler chicken L-carnitine improved average daily gain and reduced the abdominal fat content. These trials also implied dosages of L-carnitine of 50 to 100 mg per kg feed.
4. Reproductive and physical performance of **racing pigeons** were improved by daily administrations of about 80 mg of L-carnitine per animal.
5. Dietary L-carnitine supplementations affected parameters of blood plasma and improved the L-carnitine status. The concentration of blood glucose was increased and the concentration of free fatty acids was decreased in some studies. L-carnitine concentrations in blood plasma and milk were regularly increased. When L-carnitine was administered to **horses** for several weeks its concentrations in skeletal muscle were also elevated.
6. In feeding trials with L-carnitine in adult ruminants possible losses of carnitine in the rumen due to microbial degradation should be taken into account.
7. For most domestic species and for most of the reported effects no clear dose/response relationship exists. Further studies are probably required to more clearly define the conditions under which L-carnitine supplementations may be expected to be beneficial.

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